Volume 56, Number 1

February 1982

Northwest Science

1 Small Mammals of a Bitterbrush-Cheatgrass Community
K. A. Gano and W. H. Rickard

8 The Trichoptera of Montana with Distributional and Ecological Notes
George Roemhild

14 Internal Parasites of Coyotes (**Canis latrans**) in Washington and Idaho
William J. Foreyt and Kristine M. Foreyt

17 Generic Relationships of **Phenacomys albipes**
Murray L. Johnson and Chris Maser

20 Population Structure of the Crab **Hemigrapsus oregonensis** (Brachyura, Grapsidae) in Yaquina Bay Estuary, Oregon: I. Reproductive Cycle
Robert E. Batie

27 Precipitation Variability in the Columbia Basin of Washington
J. D. Helvey and W. B. Fowler

34 Postburn Regrowth of Shrubs Related to Canopy Mortality
T. E. Owens

41 Self-Revegetation of Disturbed Ground in the Deserts of Nevada and Washington
W. H. Rickard and R. H. Sauer

48 Algal Growth Stimulus by Phosphorus in Flathead Lake, Montana, Sediments
William B. Perry and Jack A. Stanford

53 Photoperiod Experiments on the American Robin (**Turdus migratorius** L.)
D. Lynne Kemper and J. Mary Taylor

58 Contributions to Paleontology by an Early Montana Physician
Thomas H. Lewis

62 The Non-Fisheries Biological Resources of the Hanford Reach of the Columbia River
W. H. Rickard, W. C. Hanson, and R. E. Fitzner

77 Association News

Official Publication of the Northwest Scientific Association

US ISSN 0029 344X

Northwest Science

Volume 56, Number 1, February 1982

The Northwest Scientific Association is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to Northwest Science, is open to individual persons for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 3000 students or more, $40. All other subscribers, $20 per year. Sustaining membership, $25 per year for individual persons and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Payment should be made to the Treasurer.

Editor **John W. Weber**
Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164-2910

Officers of the Association

President **John H. Perkins**
Walla Walla College
College Place, Washington
(1983)

Vice-President **Steven F. Arno**
USDA Forest Service
Missoula, Montana (1983)

Secretary **Robert L. Carr**
Eastern Washington University
Cheney, Washington (1984)

Treasurer **Robert J. Jonas**
Department of Zoology
Washington State University
Pullman, WA 99164-4220 (1983)

Past President **James R. Chambers**
Walla Walla College
College Place, Washington
(1983)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Back
University of British Columbia
Vancouver, British Columbia
(1985)

Charles R. Hatch
University of Idaho
Moscow, Idaho (1983)

Janet E. Hohn
U.S. Fish and Wildlife Service
Portland, Oregon (1983)

Denis P. Lavender
Oregon State University
Corvallis, Oregon (1984)

Roger del Moral
University of Washington
Seattle, Washington (1983)

Don Minore
U.S. Forest Service
Corvallis, Oregon (1984)

Richard J. Naskali
University of Idaho
Moscow, Idaho (1984)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

Ronald H. Sauer
Battelle Northwest Laboratories
Richland, Washington (1984)

Steven R. Seavy
Lewis and Clark College
Portland, Oregon (1985)

Kareen Sturgeon
Linfield College
McMinnville, Oregon (1985)

J. Mary Taylor
University of British Columbia
Vancouver, British Columbia
(1983)

Robert Zasoski
University of Washington
Seattle, Washington (1984)

Donald B. Zobel
Oregon State University
Corvallis, Oregon (1983)

*Term of office expires in the year given in parentheses

PUBLISHED QUARTERLY BY WASHINGTON STATE UNIVERSITY PRESS
WITH COLLABORATION OF NORTHWEST SCIENTIFIC ASSOCIATION

K. A. Gano
and
W. H. Rickard
Battelle Pacific Northwest Laboratories
Richland, Washington 99352

Small Mammals of a Bitterbrush-Cheatgrass Community

Abstract

Small mammals were live-trapped in burned and unburned segments of a bitterbrush-cheatgrass community during the years 1974-1979. Results indicate that the shrub-dominated unburned area supports about three times as many small mammals as the cheatgrass-dominated burned area. Species composition was similar in both areas with the exception of one ground squirrel (*Spermophilus townsendii*) captured on the unburned area. Other species caught were the Great Basin pocket mouse (*Perognathus parvus*), deer mouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*), and the western harvest mouse (*Reithrodontomys megalotis*).

Introduction

The bitterbrush-cheatgrass community is located in the southeastern part of the Department of Energy's Hanford Site in Benton County, Washington, and occupies about 31,000 ha (Fig. 1). At the present time, the community is mostly undisturbed, but it was grazed by livestock prior to 1943. Large construction projects like the Fast Flux Test Facility (FFTF) and the commercial nuclear power projects of the Washington Public Power Supply System (WPPSS) have recently been constructed and now occupy a part of this community. In the absence of grazing livestock, wildfires make up the most drastic and widespread disturbance. Fire swept across the southeastern section of the Hanford Site in the summer of 1963, burning 4038 ha (O'Farrell *et al.*, 1971). The same area burned again in 1970 along with some additional, previously unburned land. Burning effectively kills the xerophytic shrubs, especially bitterbrush (*Purshia tridentata* (Pursh) DC.) and sagebrush (*Artemisia tridentata*, Nutt). Herbaceous understory plants consisting mostly of cheatgrass (*Bromus tectorum* L.) reinvade burned areas and dominate the vegetation for many years (Rickard and Sauer, in press). Bitterbrush and sagebrush, however, are very slow to reinvade, and the time required for these shrubs to attain their previous dominance is unknown.

This investigation compares small mammal populations trapped in the burned and the unburned parts of the bitterbrush-cheatgrass community. The study began in 1974 and live-trapping was conducted through the spring of 1979. The purpose was to establish species composition and relative abundance of small mammals in two adjacent but vegetatively different habitats.

Methods

Small mammal populations were investigated in recently burned and unburned parts of the bitterbrush-cheatgrass community using a live trap recapture method. Two study plots were established in the summer of 1974, each gridded with 100 traps

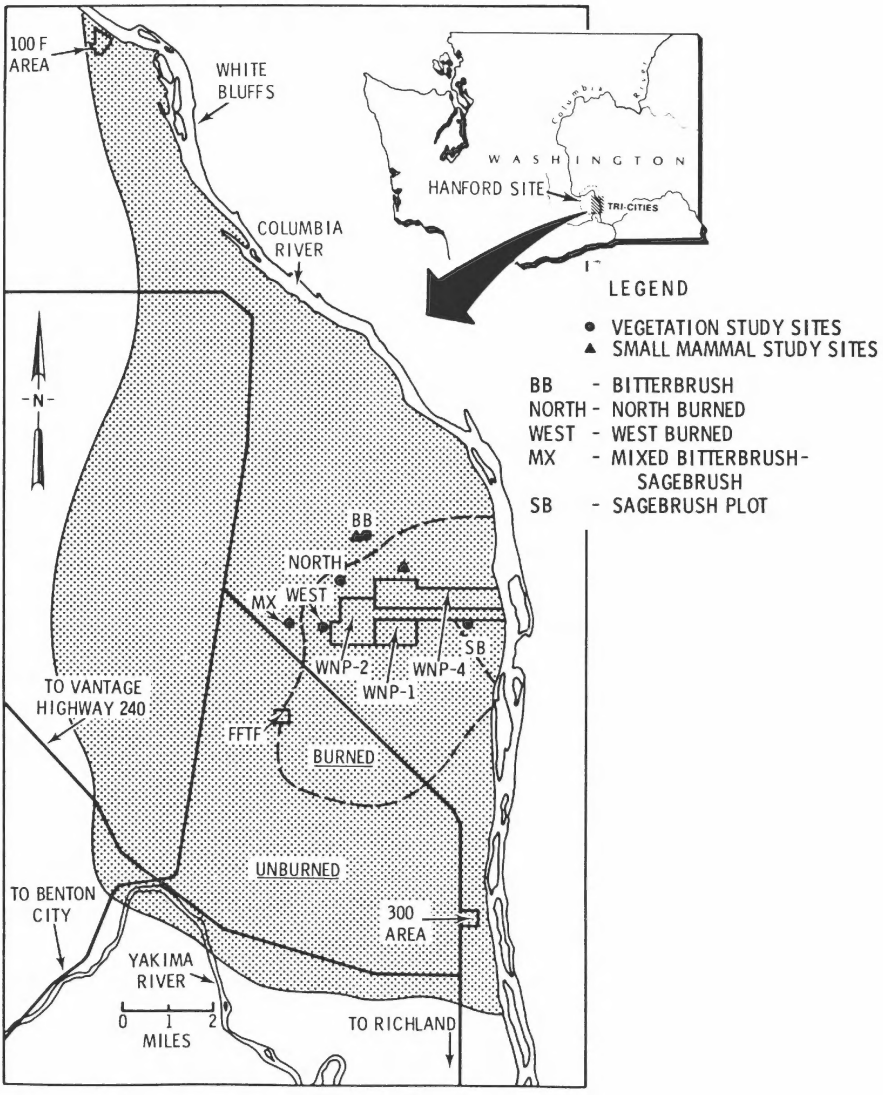


Figure 1. Southeastern part of the U.S. DOE Hanford Site showing the extent of the Bitterbrush-Cheatgrass community, shaded; the location of the WPPSS (Washington Public Power Supply System) property, and the location of the study plots.

spaced at 10 m intervals. One plot was located in a relatively undisturbed stand representative of the unburned community, and the other was located in an area that had burned in 1970. Both plots were a mile or more from the WPPSS construction site. We believe mammal behavior was unaffected by construction noises and dust.

Trapping was conducted according to the method employed by O'Farrell (1975).

Sherman live traps were placed one to a grid point and shielded by a large metal can (10 x 10 x 30 cm). A 24-gauge galvanized steel tent 30 cm wide, 40 cm long, and 25 cm high at the peak shielded the can and the trap, providing protection from heat, wind, and rain. Each trap was supplied with enough seeds to prevent animal torpor and contained some soft fiber for nesting during overnight confinement. Both plots were serviced for three consecutive days during each trapping session by the same pair of investigators. During the first year, trapping sessions were conducted monthly to establish the yearly cycles of small mammal activity. Trapping effort in the following years was reduced to a minimum of two sessions per year. Trapping was conducted in spring to record peak activity during the breeding season and again in late summer to record any recruitment of young into the population. Mice were individually marked by toe amputations and released near the point of capture. Individual animals were weighed alive using a spring tension scale accurate to 0.5 g.

Results and Discussion

In the period 1974 to 1979, 12,200 trap nights were recorded. Five hundred sixty-one individual animals representing five species were trapped, marked, and released. The great basin pocket mouse (*Perognathus parvus*) was the most abundant animal trapped, with 469 individuals captured. Second was the deer mouse (*Peromyscus maniculatus*), with 68 individuals. The northern grasshopper mouse (*Onychomys leucogaster*) was represented by only 15 individuals, the western harvest mouse (*Reithrodontomys megalotis*) by eight individuals, and the Townsend ground squirrel (*Spermophilus townsendii*) by one individual. There were more animals trapped in the unburned community than in the community with a recent fire history (Table 1).

TABLE 1. Total number of individual small mammals captured and released on burned and unburned parts of the bitterbrush-cheatgrass community 1974-1979.

Species	Unburned Plot	Burned Plot	Total
Pocket mouse	362	107	469
Deer mouse	54	14	68
Grasshopper mouse	10	5	15
Harvest mouse	6	2	8
Townsend ground squirrel	1	0	1
Total	433	128	

TABLE 2. Spring and summer catch of pocket mice in unburned and burned communities during the years 1974 to 1979.

Year	Unburned (Control) Spring	Unburned (Control) Summer	Burned Spring	Burned Summer
1974	—	46	—	29
1975	36	27*	27	13*
1976	52	53	8	2
1977	43	30	7	14
1978	15	56	1	5
1979	64	—	9	—
Average	42	42	10	13

*Trapping session conducted in July

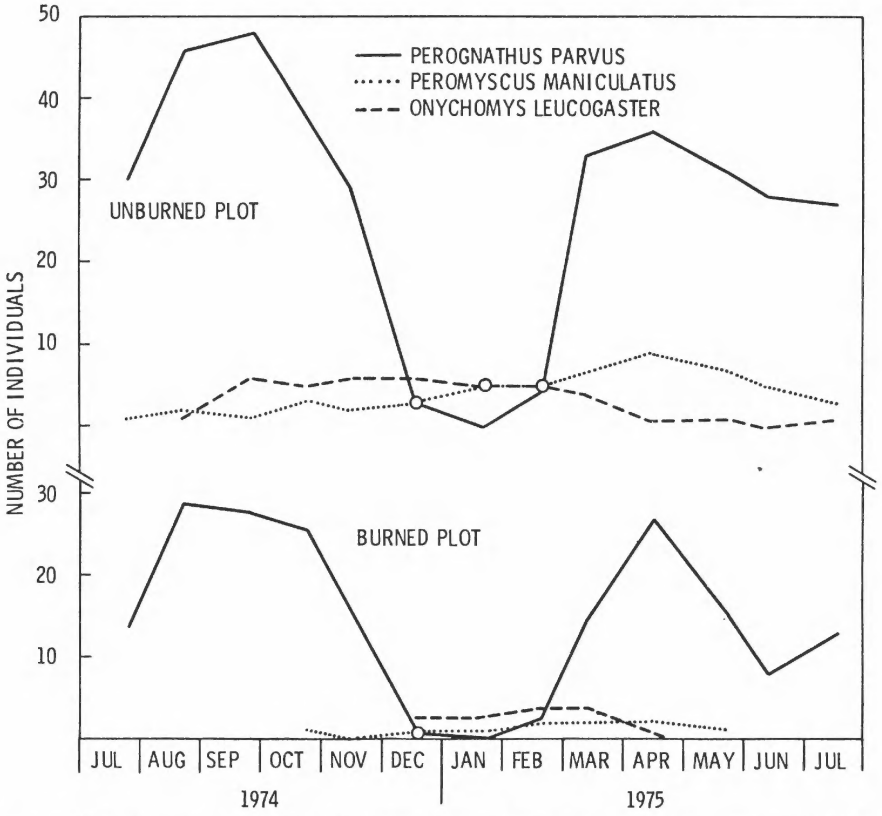


Figure 2. Comparison of seasonal fluctuations of small mammal populations 1974 and 1975 in burned and unburned bitterbrush-cheatgrass communities.

The most abundant small mammal trapped in the bitterbrush-cheatgrass community was again the pocket mouse. The yearly cycle of activity for the pocket mouse begins in March and early April as adults emerge from winter torpor to breed (O'Farrell *et al.*, 1975). A second population peak is usually observed in late summer with the recruitment of young into the population (Fig. 2). The trap catches made during these two peak seasonal activity periods during the years 1974 to 1979 are summarized in Table 2.

These data provide an estimate of the number of pocket mice active on the study plots at the time of trapping. Assuming that the effective area of a trapping grid was one hectare and that the vulnerability of pocket mice to trapping was high, we estimated that the pocket mouse population was about three times more dense on the unburned plot than on the burned plot. The population showed greater year to year fluctation on the burned plot than on the unburned plot. The spring catch of pocket mice was lowest in 1978 when only 15 animals were trapped in the unburned plot and only one on the burned plot. This small catch may have been the result of the severe drought and resulting low plant productivity of the 1977 growing season. Only 3.07

cm of rain fell between October 1976 and April 1977, with only 10 $g/m^2/yr$ of herbaceous phytomass produced (Rickard and Sauer, in press). Nevertheless, the pocket mouse population quickly recovered, as 56 animals were trapped on the unburned plot in late summer of 1978. Forty-four of the animals captured were classified as young of the year. This increase was apparently in response to the higher precipitation (14.35 cm) and resulting higher phytomass of the 1978 growing season. The average rainfall for the growing season (October to May) at the Hanford Site is 13.0 cm (Stone *et al.*, 1972). The high correlation between autumn-spring precipitation and pocket mouse abundance has been pointed out by O'Farrell *et al.* (1975) and Dunigan *et al.* (1980).

Some additional insight concerning the population dynamics of the pocket mouse population can be obtained by noting the number of marked individuals recaptured after emerging from winter dormancy. Table 3 shows the number of individuals recaptured on both plots after one or two winters. The greatest number of spring recaptures came from the 1974 catch with 42 percent recaptured on the unburned plot and 18 percent on the burned plot after the first winter. However, only 8 percent (unburned) and 4 percent (burned) of the original 1974 catch were captured after the second winter. The only other year class for which recaptures in two successive years were obtained was that of 1976, in which only 2 percent recaptures after the second winter were obtained in the unburned plot.

TABLE 3. Total number of pocket mice marked and retrapped after 1-2 winters.

	1974	1975	1976	1977	1978	1979
Unburned 1974	48	20(42%)	4(8%)			
Burned 1974	28	5(18%)	1(4%)			
Unburned 1975		22	5(23%)			
Burned 1975		11	1(9%)			
Unburned 1976			99	18(18%)	2(2%)	
Burned 1976			7	1(14%)		
Unburned 1977				49	8(16%)	
Burned 1977				18	—	
Unburned 1978					60	19(32%)
Burned 1978					6	3(50%)
Unburned 1979						45
* Burned 1979						6

*Trapping data represents 1 trap session in spring.

These recapture percentages are probably conservative estimates of survival because only two trapping sessions per year were used. Although the two peak activity periods for pocket mice were used, spring (April-May) and late summer (August-September), recapture percentages could be much greater than indicated; nevertheless, no marked animals were recaptured after three winters.

On the average, more males than females were caught, a possible indication of the male's slightly greater mobility (O'Farrell *et al.*, 1975). Male pocket mice on the average weighed more than females (Table 4). When comparing burned and unburned

TABLE 4. Live weights of pocket mice (gm) in unburned and burned communities during the Spring Season.

	Unburned				Burned			
	Males		Females		Males		Females	
	n	$\bar{x}$ +SE	n	$\bar{x}$ +SE	n	$\bar{x}$ +SE	n	$\bar{x}$ +SE
1975	28	18.5± .3	8	14.4± .2	13	17.0± .5	14	14.3± .3
1976	23	18.4± .4	29	17.6± .5	5	18.1± .6	3	17.0±1.3
1977	25	19.0± .4	18	15.2± .3	5	19.0± .8	2	18.5±0
1978	9	20.5± .5	6	17.8±1	No Captures		1	15.5
1979	30	18.5± .4	34	16.8± .3	4	19.4± .4	5	16.1± .5

communities, a Student's t-test showed no significant differences in weights of like sexes.

Deer Mouse Populations

Deer mouse populations were much lower than pocket mouse populations. Nevertheless, the unburned community yielded about three times more deer mice than the burned community. The spring catch of deer mice was consistently greater than the summer catch with no deer mice captured on the burned community during summer trapping. Assuming an effective trapping area of one hectare and a high trap efficiency for deer mice, we estimated that about six deer mice per hectare were present on the unburned bitterbrush-cheatgrass community and only two per hectare on the burned community.

The small mammal species composition of the bitterbrush-cheatgrass community is like communities elsewhere on the Hanford Site (Kritzman, 1970). O'Farrell *et al.* (1975) used a stochastic model to estimate the pocket mouse population in a sagebrush-cheatgrass community. Over a five year period (from 1967-1971), the April population ranged between 20 and 75 mice per hectare. Hedlund *et al.* (1975) estimated the trappable pocket mouse population of a cheatgrass community at 30 per hectare during April 1974.

Summary

The findings of our investigation indicate that the cheatgrass-dominated plant community does not support as dense a population as the shrub community. According to Battelle researchers at the Arid Lands Ecology Reserve, small mammal populations in sagebrush-bluebunch wheatgrass communities (*Artemisia tridentata-Agropyron spicatum*) are relatively unaffected when fire removes the shrub cover. The role that shrubs play in providing "prime" habitat for pocket mice has not been investigated. Shrubs may play an important role by providing protection from vertebrate predators. The role that herbaceous vegetation structure plays in impeding overground movements of pocket mice likewise has not been investigated. Uniformly dense stands of cheatgrass may deter pocket mice from using such an area by hindering their aboveground movements. If mobility of the mice is reduced, breeding success might also be reduced, resulting in a smaller population. Possibly the population estimate may be inherently low on the cheatgrass plot because of the conceivable difficulty animals may have in finding the traps in dense herbaceous vegetation.

The ecological role of small mammals in the bitterbrush-cheatgrass community

is that of prey for higher trophic level animals such as the gopher snake, coyote, badger, and raptorial birds. A comparative diet study of cheatgrass and shrub-dominated communities may help answer the question, "Why are there fewer small mammals in the cheatgrass community?" In addition, an energetics study comparing the two communities and available energy sources (food items) to small mammals could help explain the difference in population density.

Acknowledgment

This work was performed under the sponsorship of the Washington Public Power Supply System, Richland, Washington. D. T. McCullugh and M. A. Rumble provided technical assistance.

This paper was prepared for publication with Department of Energy support as part of the Terrestrial Ecology Studies Program under contract DE-AC06-76RL0 1830.

Literature Cited

Dunigan, P. F. X., Jr., W. Lei, and W. H. Rickard. 1980. Pocket mouse population response to winter precipitation and drought. Northw. Sci. 54:289-295.

Hedlund, J. D., D. T. McCullugh, and W. H. Rickard. 1975. Mouse populations on knob and kettle topography in south-central Washington. Northw. Sci. 49:253-360.

Kritzman, E. B. 1970. Niche Fit and Overlap of *Peromyscus maniculatus* and *Perognathus parvus* in Eastern Washington. Univ. of Washington, M.S. thesis.

O'Farrell, T. P. 1975. Seasonal and altitudinal variations in populations of small mammals on Rattlesnake Mountain, Washington. Amer. Midl. Nat. 94:190-204.

———, R. J. Olson, R. O. Gilbert, and J. D. Hedlund. 1975. A population of great basin pocket mice, *Perognathus parvus*, in the shrub-steppe of south-central Washington. Ecol. Monogr. 45:1-28.

———, W. H. Rickard, and K. R. Price. 1971. Energy flux during the 1970 wildfire. BNWL-1550. Vol. 1, Part 2:1.2-1.3. Battelle Pacific Northwest Laboratories Annual Report for 1970, Richland, WA 99352

Rickard, W. H., and R. H. Sauer. In press. Plant communities of the sagebrush-bitterbrush zone of south-central Washington. Northw. Sci.

Stone, W. A., D. E. Jenne, and J. M. Thorp. 1972. Climatography of the Hanford Area. BNWL-1605. Battelle, Pacific Northwest Laboratories, Richland, WA 99352.

Received March 27, 1980
Accepted for publication May 21, 1980

George Roemhild
Department of Biology
Montana State University
Bozeman, Montana 59717

The Trichoptera of Montana with Distributional and Ecological Notes[1]

Abstract
The known Montana Trichoptera is comprised of 14 families, 69 genera, and 222 species. Seventy-eight species are reported from Montana for the first time. One hundred sixty-seven species (77 percent of total) are known to occur on both sides of the continental divide, 22 species (10 percent) occur on the east side only, and 29 species (13 percent) occur only west of the divide.

Introduction

Montana is a large state with a wide variety of ecological conditions. Elevation ranges from 549 m to 3902 m, and rainfall varies from less than 28 cm to more than 254 cm per year. A variety of vegetative types, ranging from cold desert through prairie grasslands, intermountain parkland, and mountain forest to tundra, occur within the state. Because of this diversity in conditions, along with the state's location astraddle the continental divide, state species lists may provide relevant information to zoogeographers about faunal relationships to both the east and the west.

Listed are 222 species of caddisflies taken to date in Montana. Most of these have been collected by the author and are in the Montana State University collection. Newell's first paper (1970) listed 100 species of caddisflies from the state, and his 1971 paper added 18 species to the list. Newell and Potter (1973) discuss the distribution and emergence of 110 species predominantly from the western part of the state. A few of the species listed have not been collected by either the author or by Newell, but have been cited as occurring in the state by Ross (1938, 1944), Nimmo (1971, 1977), or Blickle (1979).

Several papers have recently appeared dealing with Trichoptera distribution in the northwest and Rocky Mountain area. Harris, Lago, and Carlson (1980) have listed 102 species from North Dakota; Anderson (1976) lists 282 species from Oregon; Newell and Minshall (1977) list 84 species from southeastern Idaho; Nimmo and Scudder (1978) list 248 species from British Columbia; and Nimmo (1971, 1974, 1977) has published on the members of several families of trichopterans which occur in Alberta. Blickle (1979) gives the North American distribution for microcaddisflies (Hydroptilidae).

The species names in the following list are followed by notes concerning ecological preferences and distribution within the state and in nearby areas as cited by the authors above.

Montana Trichoptera
Columns after species names are (1) Montana distribution: E—east of continental divide, W—

[1]Journal paper number 1043, Montana Agricultural Experiment Station.

west of divide; (2) Altitudinal distribution: A—alpine, I—intermountain, P—prairie; (3) Water temperature preference: C—cold, V—variable, W—warm; (4) Habitat affinity: L—lake, P—pond, R—river, S—stream; (5) Relative abundance: A—abundant, C—common, R—rare; (6) Northwest distribution: A—Alberta, B—British Columbia, I—Idaho, N—North Dakota, O—Oregon. *After species denotes new Montana record.

Hydroptilidae	1.	2.	3.	4.	5.	6.
	1.	2.	3.	4.	5.	6.
	1.	2.	3.	4.	5.	6.
	1.	2.	3.	4.	5.	6.
	1.	2.	3.	4.	5.	6.
	1.	2.	3.	4.	5.	6.
Hydroptilidae						
Agraylea multipunctata Curtis	EW	IP	W	L	C	BNO
saltesea Ross	EW	IP	W	LR	C	O
Hydroptila ajax Ross						O
allosi Blickle	W	I	W	P	R	
arctia Ross*	EW	I	W	R	C	B
argosa Ross*	E	IP	W	R	C	O
consimilis Morton	E	P	W	R	R	BO
hamata Morton	E	I	W	R	R	O
rono Ross	E	I			R	O
waubesiana Betten*	E	P	W	RL	R	N
xera Ross*	E	I	W	RL	R	BO
Ithytrichia clavata Morton*	E	P	W	R	R	B
Leucotrichia pictipes (Banks)	EW	I	W	R	C	O
Mayatrichia ayama Mosely*	E	P	W	S	R	
Neotrichia ersitis Denning						
halia Denning						
Ochrotrichia alsea Denning & Blickle	W	I	V	R	R	O
oregona (Ross)						IO
potomus Denning*	E	P	W	R	R	
stylata Ross	E	I	W	R	R	ION
Orthotrichia cristata Morton						B
Oxyethira aeola Ross						BO
coercens Morton						
dualis Morton						O
Zumatrichia notosa (Ross)	E	I	W	R	R	
Helicopsychidae						
Helicopsyche borealis (Hagen)	EW	I	W	S	A	ION
Hydropsychidae						
Arctopsyche grandis (Banks)	EW	IP	C	RS	A	BIO
Cheumatopsyche campyla Ross	EW	IP	VW	RS	A	BION
enonis Ross*	E	P	W	R	C	IO
gracilis (Banks)	EW	I	V	R	R	BN
lasia Ross	E	P	W	RS	C	N
logani Gordon & Smith*	E	I	W	R	R	
oxa Ross*	E	P	W	S	R	
pasella Ross*	E	I	W	L	R	NO
pettiti (Ross)	EW	IP	W	PSR	C	BION
smithi Gordon*	E	IP	W	LR	C	N
speciosa (Banks)*	E	I	V	R	R	N
Hydropsyche bidens Ross*	E	P	W	R	R	N
cockerelli Banks	EW	I	W	R	R	IO
jewetti Denning	EW	I	V	R	C	
occidentalis Banks	EW	IP	VW	RSL	A	BO
oslari Banks*	EW	I	VW	RS	A	BIO
placoda Ross	E	P	W	R	R	
separata Banks	E	P	W	R	C	
simulans Ross*	E	P	W	RP	R	N
tana Ross	EW	I	V	R	R	
Parapsyche almota Ross	W	AI	C	RS	R	BIO
elsis Milne	EW	I	V	RS	C	BIO
Potamyia flava (Hagen)	EW	I	V	R	R	N
Symphytopsyche bifida (Banks)	EW	P	W	R	C	BIN
bronta (Ross)	E	P	W	R	C	N
slossonae (Banks)*	EW	I	V	S	R	N

Rhyacophilidae						
Rhyacophila acropedes Banks	EW	I	CV	SR	C	ABIO
alberta Banks	W	A	C	S	R	ABI
alexanderi Denning	W				R	
angelita Banks	EW	AI	C	S	C	ABIO
bifila Banks	EW	I	C	SR	A	ABIO
coloradensis Banks	EW	I	C	SR	A	ABI
ebria Denning	W	A	C	S	R	B
gemona Ross	W				R	
glaciera Denning	EW	A	C	S	R	A
hyalinata Banks						BIO
kernada Ross*	E	I	C	S	R	B
narvae Navas	EW	AI	C	S	C	AIO
newelli Denning	W				R	B
oreta Ross*	E	A	C	S	R	O
pellisa Ross	EW	I	C	S	C	ABIO
robusta Schmid*	E	A	C	S	R	AB
tucula Ross	W	A	C	S	R	ABO
unimaculata Denning	W			S	R	B
vaccua Milne	W	I	V	S	C	ABIO
vagrita Milne	EW	A	C	S	R	ABIO
valuma Milne	W	A	C	S	R	BO
vao Milne	EW	I	V	S	R	ABIO
vemna Milne	W				R	ABO
verrula Milne	EW	I	V	S	C	ABIO
vobara Milne	W	A	C	S	R	AB
vocala Milne	EW	I	V	SR	C	ABIO
vuzana Milne	W	I	C	R	R	BO
wallowa Denning	EW	A	C	S	C	O
Glossosomatidae						
Agapetus montanus Denning	EW	I	V	SR	R	I
Anagapetus debilis Ross	EW	AI	C	S	C	ABIO
Culoptila cantha (Ross)	E	P	W	RL	C	
Glossosoma alascense Banks	EW	I	V	SR	C	ABIO
excitum Ross	E	I	V	C	R	BO
idaho Ross	EW	I	V	S	R	BI
intermedium (Klapalek)*	E	A	C	S	R	AI
montana Ross	EW	I	V	SR	C	AO
parvulum Banks*	E	I	V	R	R	
penitum Banks	W	I	V	S	C	BO
traviatum Banks	EW	I	V	S	C	IO
velona Ross	EW	I	V	R	A	ABIO
verdona Ross	EW	AI	C	SR	C	ABIO
Protoptila coloma Ross*	E	I	V	SR	C	I
erotica Ross*	E	IP	W	SR	R	
tenebrosa (Walker)					R	A
Phryganeidae						
Agrypnia colorata Hagen*	E	P	W	LP	C	BN
glacialis Hagen*	E	A	C	P	R	BN
improba (Hagen)*	EW	A	C	L	R	BON
straminea Hagen	EW	IP	V	PR	R	N
Banksiola crotchi Banks*	W	I	V	R	R	BON
Phryganea cinerea Walker	EW	IP	W	LR	C	BON
Ptilostomis semifasciata (Say)*	E	P	W	S	R	BN
Polycentropodidas						
Neureclipsis bimaculata (Linneaus)*	EW	P	W	R	R	BN
crepuscularis (Walker)*	W	I	V	R	R	
Nyctiophylax affinis (Banks)*	W	I	V	L	R	B
moestus Banks*	E	P	W	L	R	B
Polycentropus cinereus Hagen	EW	IP	W	L	C	BION
denningi Smith*	W	I	V	R	R	O
flavus (Banks)	W				R	BN
halidus Milne*	W	I	C	S	R	BO
variegatus Banks*	W	I	V	S	R	BO
Psychomyiidae flavida Hagen	EW	I	VW	RS	A	ION
Molannidae						
Molanna flavicornis Banks	EW	P	W	L	C	BN

Leptoceridae						
Ceraclea annulicornis (Stephens)	EW	I	V	R	C	IO
cancellatus (Betten)*	W	I	W	L	R	BN
cophus (Ross)*	E	I	W	R	R	BI
tarsipunctatus (Vorhies)*	EW	IP	CVW	RS	C	IO
transversus (Hagen)*	W	I	W	L	R	IO
resurgens (Walker)*	W	I	V	R	R	BON
Mystacides alafimbriata Griffin	EW	A	C	S	R	BIO
longicornis (Linneaus)	EW	I	V	L	R	N
sepulchralis (Walker)	W	I	W	L	R	BN
Nectopsyche albida (Walker)*	E	P	W	S	R	BIO
candida (Hagen)*	E	P	W	S	R	N
diarina (Ross)*	E	IP	W	SR	C	IN
*lahontenesis**	E	P	W	S	R	
Oecetis avara (Banks)	EW	IP	VW	SL	C	BON
disjuncta (Banks)*	EW	IP	W	SL	C	
immobilis (Hagen)	EW	IP	W	SL	C	BN
inconspicua (Walker)	EW	IP	W	SL	C	BON
ochracea (Curtis)	EW	P	W	L	A	BN
Triaenodes grisea (Banks)	EW	P	W	L	C	BON
frontalis Banks	EW	P	W	L	C	I
tardus Milne	W	I	V	L	R	BON
Philopotamidae						
Chimarra utahensis Ross*	W	I	W	P	R	O
Dolophilodes aequalis (Banks)	EW	I	V	S	A	ABIO
dorca (Ross)*	W	I	V	S	C	BO
novusamericanus (Ling)	W	I	V	S	C	ABO
pallidipes (Banks)	EW	AI	C	S	C	BO
Wormaldia gabriella (Banks)	EW	I	C	S	C	ABIO
occidea (Ross)	W	A	C	S	R	BO
Brachycentridae						
Amiocentrus aspilus (Ross)	EW	IP	VW	SR	A	BIO
Brachycentrus americanus (Banks)	EW	I	V	SR	A	BION
occidentalis Banks	EW	IP	V	SR	A	BO
Micrasema bactro Ross	W				R	BO
Lepidostomatidae						
Lepidostoma aporna Denning*	E	I	W	R	R	
cascadense (Milne)	EW	I	V	S	R	B
knowltoni Ross	EW	I	V	R	C	O
pluviale (Milne)*	E	IP	VW	SR	A	BIO
podager (McLachlan)	EW	I	V	S	R	IO
quercina Ross*	E	I	C	S	R	BO
rayneri Ross*	E	P	W	S	R	BO
roafi (Milne)	W	I	V	S	R	BO
spicata Denning	W	I	V	S	R	
strophis Ross	EW	I	W	S	R	BIO
unicolor (Banks)*	EW	I	V	S	C	BION
veleda Denning	EW	IP	CW	SRL	C	O
Goeridae						
Goeracea genota (Ross)	W	AI	C	S	C	BO
Goereilla baumanni Denning	W	AI	C	S	R	
Limnephilidae						
Amphicosmoecus canax (Ross)	EW	I	C	S	R	ABIO
Anabolia bimaculata (Walker)*	EW	I	V	S	R	ABN
Apatania chasica Denning	EW	I	C	SR	C	I
comosa Denning	EW	IP	V	SR	C	I
shoshone (Banks)	E	A	C	S	C	AB
zonella (Zetterstedt)						AB
Asynarchus aldinus (Ross)*	W	A	C	L	R	ABON
Chyranda centralis (Banks)	EW	AI	C	S	C	ABIO
Clistoronia magnifica (Banks)	W	A	C	S	R	ABO
Cryptochia furcata Denning	W	A	C	S	R	B
Dicosmoecus atripes (Hagen)*	EW	A	C	S	R	ABO
jucundus Banks*	EW	I	C	SP	C	ABO
gilvipes (Hagen)*	E	I	C	S	R	BO
schmidi Wiggins	EW	A	C	S	R	B

Ecclisomyia conspersa Banks	EW	AI	C	SR	A	ABO
maculosa Banks	W	A	C	L	C	ABO
simulata Banks	W	AI	C	S	R	I
Glyphopsyche irrorata (Fabricius)	EW	I	V	S	R	ABO
Hesperophylax consimilus (Banks)*	EW	AI	V	SL	C	AIO
incisus (Banks)*	E	AI	V	RL	R	ABIO
occidentalis (Banks)*	E	IP	V	S	C	AB
Homophylax acutus Denning	W	A	C	S	R	A
flavipenni Banks	E	A	C	S	R	B
Imania bifosa Ross	E	A	C	L	R	AB
cascadus (Ross)	W	A	C	S	R	ABO
tripunctata (Banks)						AB
Lenarchus brevipennis (Banks)	E	A	C	S	R	ABIO
Limnephilus alberta Denning*	W	A	C	S	R	AB
canadensis Banks*	E	I	V	S	R	ABON
cockerelli Banks*	E	A	C	S	R	
externus Hagen	EW	IP	VW	L	C	AON
fagus Ross*	E	I	C	R	R	BO
frijole Ross*	E	P	W	R	R	IO
harrimani Banks	E	A	C	S	R	BO
hyalinatus Hagen*	EW	P	W	SP	C	ABON
loloensis Smith	W	A	C	S	R	
neoaculatus Denning*	E	I	V	S	R	
ornatus Banks	W	I	V	R	R	N
picturatus McLachlen*	E	A	C	L	R	AB
productus Banks*	E	I	C	S	R	O
secludens Banks*	E	P	W	R	R	ABON
spinatus Banks*	E	P	V	SL	C	ABIO
taloga Ross*	E	P	W	S	R	
Neophylax occidentis Banks*	EW	A	C	S	R	BIO
rickeri Milne	EW	I	C	S	R	AO
splendens Denning	EW	A	C	L	R	IO
Neothremma alicia Banks	EW	A	C	S	R	AIO
Oligophlebodes minuta (Banks)*	E	AI	C	S	R	IO
mostbento Schmid*	E	A	C	S	R	
ruthae Ross	EW	AI	C	S	R	AIO
sierra Ross*	W	I	C	R	R	
sigma Milne*	W	I	C	R	R	
zelti Nimmo*	EW	A	C	S	R	A
Onocosmoecus unicolor (Banks)	EW	I	C	RS	C	BIO
Psychoglypha alascensis (Banks)	W	I	C		R	ABO
prita (Milne)	EW	A	C	S	R	AO
subborealis (Banks)	EW	AI	C	SR	C	BIO
Pycnopsyche guttifer (Walker)						AN
Rossiana montana Denning	W	I	C	S	R	B

Discussion

Two hundred and four of the 222 species listed have been collected by the author during the past five years. Collections were made by sweeping vegetation along streams, ponds, and lakes; by picking individual insects from bridges and other objects near the water; and from light-trap collections made at various locations throughout the state. Most collections by the author were made east of the continental divide because Newell and co-workers (1970, 1971, 1973) did most of their collecting west of the divide. In this regard, members of the family Hydroptilidae, the micro-caddisflies, were not assiduously collected in the west so that the data presented here are certainly prejudiced in regard to the distribution of this group.

Of the 18 Montana species not collected by the author, some were collected by Newell *et al.* (1970, 1971, 1973), some reported by Blickle (1979, 1980), some by Ross (1938, 1944), and some by Nimmo (1971, 1974, 1977).

Because of the large area of the state and limited amount of collecting time available, there are several geographic regions which probably are not adequately covered.

The southwestern, southeastern, and northeastern regions are such places. Recent findings of rare larvae in some of these areas indicate that more work is needed. Our most recent work in alpine areas has yielded a number of new records for the state, especially within the family Limnephilidae.

Altitudinal distribution as noted in the table is quite straightforward. Higher, colder water in the state is dominated by limnephilids and the "mountain caddisflies," Rhyacophilidae and Glossosomatidae. Waters which we have designated "variable" include most of our intermountain rivers and streams which support trout. Warm waters refer to prairie streams at lower elevations and also to thermally influenced waters.

Literature Cited

Anderson, N. H. 1976. The Distribution and Biology of the Oregon Trichoptera. Oregon State Univ. Agric. Expt. Stat. Tech. Bull. 134.

Blickle, R. L. 1979. Hydroptilidae (Trichoptera) of America North of Mexico. New Hampshire Agric. Expt. Stat. Bull. 509.

———. 1980. A new Oxyethira (Hydroptilidae, Trichoptera) of the aeola group; with a key to separate the five males of the group. Pan Pac Entomol. 56:101-104.

Harris, S. C., P. K. Lago, and R. B. Carlson. 1980. Preliminary survey of the Trichoptera of North Dakota. Proc. Entomol. Soc. Wash. 82(1):39-43.

Newell, R. L. 1970. Checklist of some aquatic insects from Montana. Proc. Mont. Acad. Sci. 30: 45-56.

———. 1971. Revisions to the checklist of Montana aquatic insects. Proc. Mont. Acad. Sci. 31:69-72.

———, and D. S. Potter. 1973. Distribution of some Montana caddisflies (Trichoptera). Proc. Mont. Acad. Sci. 33:12-21.

———, and G. W. Minshall. 1977. An annotated list of the aquatic insects of Southeastern Idaho, Part II: Trichoptera. Great Basin Naturalist 37(2): 253-257.

Nimmo, A. P. 1971. The adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and eastern British Columbia and their postglacial origin. Quaest. Entomol. 7:22-34.

———. 1974. The adult Trichoptera (insects) of Alberta and eastern British Columbia, and their postglacial origins. II. The families Glossosomatidae and Philopotamidae. Quaest. Entomol. 10:315-349.

———. 1977. The adult Trichoptera (insects) of Alberta and eastern British Columbia, and their postglacial origins. I. The families Rhyacophilidae and Limnephilidae. Supplement I. Quaest. Entomol. 13:25-67.

———, and G. G. E. Scudder. 1978. An annotated checklist of the Trichoptera (insects) of British Columbia. Syesis 11:117-134.

Ross, H. H. 1938. Descriptions of nearctic caddisflies (Trichoptera) with special reference to the Illinois species. Bull. Illinois Nat. Hist. Surv. 21:101-183.

———. 1944. The Caddisflies, or Trichoptera, of Illinois. Bull. Illinois Nat. Hist. Surv. 23.

Received April 14, 1980
Accepted for publication June 2, 1980

William J. Foreyt

Depatment of Veterinary Microbiology
and Pathology
Washington State University
Pullman, Washington 99164

and

Kristine M. Foreyt

Department of Veterinary Science
University of Idaho
Moscow, Idaho 83843

Internal Parasites of Coyotes (Canis latrans) in Washington and Idaho

Abstract

One hundred twenty-two wild coyotes from Washington and Idaho were examined for the presence and burdens of internal parasites. Helminth parasites of nine genera were found. *Euparyphium* sp., an echinostome trematode, was recovered for the first time from a coyote. Numbers of all parasites recovered exceeded those reported in other published surveys. Examination of feces by a sugar flotation technique (sp. gr. = 1.27) for the presence of parasite eggs and larvae underestimated the parasite populations.

Introduction

Coyotes (*Canis latrans*) harbor several genera and species of helminth parasites, many of which are common to domestic dogs (Holmes and Podesta, 1968; Samuel *et al.*, 1978; Pence and Meinzer, 1979). Wild coyote populations may act as important reservoirs for parasite infection in domestic dogs, especially in geographical areas in which coyote density is high. Our purpose was to survey parasite species composition and abundance in a high coyote density area of the Pacific Northwest, and to compare our results to other surveys in North America.

Parasite surveys of wild coyotes from several parts of the United State and Canada have been published (Erickson, 1944; Gier *et al.*, 1978; Holmes and Podesta, 1968; Pence and Meinzer, 1979; Samuel *et al.*, 1978; Thornton *et al.*, 1974), but to our knowledge, no previous studies have been reported for the Pacific Northwest. The present study is based on necropsy findings and fecal examination of 122 coyotes obtained from two counties in eastern Washington and one adjacent county in western Idaho.

Methods and Materials

Fresh carcasses of 122 coyotes were acquired from trappers in Whitman County (N = 75) and Ferry County (N = 6), Washington, and Latah County (N = 41), Idaho. All were collected between February 1979 and March 1980. The majority were obtained during winter months from open agricultural areas.

Coyotes were eviscerated and viscera were labelled and frozen for later examination. After thawing at room temperature, stomachs, cecae, and small and large intestines

were opened, scraped, and washed with tap water. Contents were diluted with additional tap water and searched for parasites grossly and with a dissecting microscope (40X). All parasites were placed in 10 percent formalin for later counts and microscopic identification. Parasites were identified in glycerine wet mounts.

Intact lungs and tracheas were available from 103 of 122 coyotes. Tracheas, bronchi, and major bronchioles were split, washed, and examined grossly for the presence of *Oslerus* (= *Filaroides*) *osleri* nodules attached to the luminal surface. Tracheal sections containing nodules were preserved in 10 percent formalin. Hearts, pulmonary arteries, and kidneys were opened and examined. Finally, a two-gram fecal sample was taken from each rectum and examined microscopically for parasite ova, oocysts, and larvae with a standard sugar flotation technique (sp. gr. = 1.27).

Results and Discussion

Numbers and species of internal parasites recovered from 122 coyotes are given in Table 1.

TABLE 1. Parasites found in 122 coyotes from eastern Washington and western Idaho.

	Location in host	No. coyotes infected No. coyotes examined (percent)	Mean intensity[a] (Range)	Percent of infected coyotes positive by fecal flotation
Protozoa				
Isospora sp.	sm. int.	21/95 (22)	—	—
Nematoda				
Toxascaris leonina	sm. int.	109/122 (89)	43.3 (1-803)	64.2
Uncinaria stenocephala	sm. int.	68/122 (56)	82.6 (1-602)	57.4
Physaloptera sp.	stomach	63/122 (52)	20.2 (1-240)	22.2
Oslerus osleri	trachea	37/103 (36)	b	35.1
Pterygondermatites cahirensis	sm. int.	12/122 (10)	9.0 (1-41)	11.1
Cestoda				
Taenia spp.	sm. int.	52/122 (43)	22.0 (1-176)	13.5
Mesocestoides sp.	sm. int.	5/122 (4)	32.2 (1-139)	0
Trematoda				
Alaria marcianae	sm. int.	12/122 (10)	30.2 (1-192)	25
Alaria arisaemoides	sm. int.	1/122 (1)	4.0	100
Euparyphium sp.	sm. int.	1/122 (1)	65.0	0

[a]Mean intensity = Mean number of worms per infected host.
[b]Worm counts were not possible because of the coiled nature of worms in the nodules.

The most numerous parasites listed in decreasing order of abundance included *Toxascaris leonina* (89 percent), *Uncinaria stenocephala* (56 percent), *Physaloptera* sp. (52 percent), *Taenia* spp. (43 percent), *Oslerus* (= *Filaroides*) *osleri* (36 percent), *Isospora* sp. (22 percent), *Pterygondermatites cahirensis* (10 percent), *Alaria marcianae* (10 percent), *Mesocestoides* sp. (4 percent), *Alaria arisaemoides* (1 percent), and *Euparyphium* sp. (1 percent) (Table 1).

Our results indicate a considerably greater mean intensity of *T. leonina* (43.3), *Physaloptera* sp. (20.2), *U. stenocephala* (82.6), and *Taenia* spp. (22.0) per coyote than has been previously reported. This difference may be due in part to the relatively high population density of coyotes in the counties surveyed. Although no statistical data are available, our data from area trappers indicate the density of coyotes at approximately 1 per 100 ha.

One coyote from Latah County, Idaho, had 65 mature *Euparyphium* sp. echinostomes.

Like *Alaria* sp., this trematode probably uses an amphibian intermediate host, but to our knowledge, it has never been reported from a coyote or other canid. Usual definitive hosts for *Euparyphium* are otters (*Lutra canadensis*) and mink (*Mustela vison*).

Pterygondermatites cahirensis is an unusual and little known parasite of wild carnivores. Although previous surveys have reported this nematode from coyotes, all reported occurrences of this parasite in coyotes have been in the southern United States (Pence and Meinzer, 1979; Thornton *et al.*, 1974). Our survey found 10 percent of the coyotes were parasitized by *P. cahirensis*, with a mean intensity of 9.0 worms (Table 1).

Trichuris sp., *Dioctophyma renale, Capillaria* sp., or *Dirofilaria* sp. adults were not recovered from the internal organs examined. Eggs of these genera were not observed in feces.

Of 103 lungs and tracheas, 36 percent had *Oslerus osleri* nodules. Only two tracheas had nodules that appeared large enough to occlude bronchial air passages significantly.

In this study, fecal examination had only limited reliability for predicting parasite infection (Table 1). The presence of *Toxascaris, Uncinaria*, and *Alaria* was most predictable with 64, 57, and 31 percent, respectively, of fecal samples of worm-positive animals exhibiting ova. Recoveries of ova of *Taenia, Physaloptera*, and *Pterygondermatites* were least reliable with 14, 22, and 11 percent, respectively, detected by fecal flotation. Larvae of *O. osleri* were noted in 35 percent of fecal samples from coyotes with tracheal nodules. No *Euparyphium* eggs were seen in the sample from one infected coyote.

Field biologists often use fecal analysis to determine parasite prevalence in wild animal populations (Samuel and Trainer, 1968; Foreyt and Trainer, 1980). Our data suggest that at least for coyote parasites, a single fecal flotation analysis underestimates numbers of infected animals and may be inaccurate or misleading for most parasites. However, fecal flotation techniques are generally considered to be the most useful method for detecting certain microscopic protozoa, such as *Isospora* spp. Fecal analysis for parasite composition is a useful technique, but necropsy support is essential for accurate parasite data.

Literature Cited

Erickson, A. B. 1944. Helminths of Minnesota canidae in relation to food habits, and a host list and key to the species reported from North America. Am. Midl. Nat. 32:358-372.

Foreyt, W. J., and D. O. Trainer. 1980. Seasonal parasitism changes in two populations of white-tailed deer in Wisconsin. J. Wildl. Manage. 44: 758-764.

Gier, H. T., S. M. Kruckenburg, and R. J. Marler. 1978. Parasites and diseases of coyotes, pp. 37-71 *in* Bekoff, M. (ed.) Coyotes: Behavior, Biology, and Management. Academic Press, New York.

Hirsch, R. P., and H. T. Gier. 1974. Multiple-species infections of intestinal helminths in Kansas coyotes. J. Parasitol. 60:650-653.

Holmes, J. C., and R. Podesta. 1968. The helminths of wolves and coyotes from the forested regions of Alberta. Can. J. Zool. 46:1193-1204.

Pence, D. B., and W. P. Meinzer. 1979. Helminth parasitism in the coyote, *Canis latrans*, from the rolling plains of Texas. Int. J. Parasitol. 9:339-344.

Samuel, W. M., and D. O. Trainer. 1968. A technique for survey of some helminth and protozoan infections of white-tailed deer. J. Wildl. Manage. 33:888-894.

———, S. Ramalingam, and L. N. Carbyn. 1978. Helminths in coyotes (*Canis latrans* Say), wolves (*Canis lupus* L.) and red foxes (*Vulpes vulpes* L.) of southwestern Manitoba. Can. J. Zool. 56:2614-2617.

Thornton, J. E., R. R. Bell, and M. J. Reardon. 1974. Internal parasites of coyotes in southern Texas. J. Wildl. Dis. 10:232-236.

Received July 2, 1980
Accepted for publication July 30, 1980

Murray L. Johnson
and
Chris Maser[1]
Puget Sound Museum of Natural History
University of Puget Sound
Tacoma, Washington 98416

Generic Relationships of Phenacomys albipes[2]

The white-faced vole (*Phenacomys albipes* Merriam, 1901) has always been included in the genus *Phenacomys*. The genus also includes the heather vole (*Phenacomys intermedius* Merriam, 1889), and has included the red tree vole (*Arborimus longicaudus* (True, 1890)). With separation of the genera *Arborimus* and *Phenacomys* (Johnson, 1973), it is germane to analyze the taxonomic status of the white-footed vole.

Phenacomys albipes is one of the rarest voles in institutional collections, despite its occurrence in northwestern California and western Oregon, where much collecting has been done. Maser and Johnson (1967) located only 28 catalogued specimens, and only 11 additional specimens have been mentioned in the literature, including examples reported by Maser and Hooven (1969) and Sherrel (1970). In addition, Maser (unpub. data) trapped 22 specimens during 1970 through 1972. Thus, our field experience has increased; our collection now totals 42 catalogued specimens.

Taylor (1915), on the basis of two specimens, suggested that the closest ally of *P. albipes* was the red tree vole (*A. longicaudus*). Howell (1926), after studying eight specimens, declined to state affinities, but considered *P. albipes* to be a distinct species within the genus *Phenacomys*.

We studied skeletal elements (N = 25), bacula (N = 8), and preserved soft parts (N = 10) of *P. albipes*. Although the series is small, analysis of relationship is possible using multiple characters (Table 1). Most of the traits that we selected were also used in comparing the heather vole (*Phenacomys*) with the red tree vole (*Arborimus*) (Johnson, 1973).

Criteria of age determination have been established: the termination of the reentrant angle of the molars becomes visible beyond the level of the alveolus at full maturity; at senescence, the occlusal pattern becomes worn and lost. It was important to compare skulls of matching age because some of the measurements change with advancing maturity. Fourteen skulls of mature individuals were studied.

On the basis of data presented in Table 1, there is little doubt that the relationship of *P. albipes* is with the *Arborimus longicaudus* complex (including *silvicola* and a new sibling species to be described elsewhere). In conformity with the International Code of Zoological Nomenclature, Article 23 (1964), the white-footed vole is placed in the genus *Arborimus* and becomes *Arborimus albipes*.

---

[1]Present address: Forest Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331.

[2]This paper is a partial contribution to the Oregon Coast Ecological Survey, Puget Sound Museum of Natural History, University of Puget Sound, Tacoma, Washington 98416.

TABLE 1. Congruity of characters: **Arborimus albipes** related to **Arborimus longicaudus** complex (A) and **Phenacomys intermedius** (B).

Character	**A. longicaudus** complex (A)	Conguence of **A. albipes**	**Phenacomys intermedius** (B)
Geographic distribution	Restricted to humid N.W. Calif. and W. Oregon	A	Boreal North America south of the Arctic
Habitat	Humid, temperate forests	A	Boreal, timberline areas
Habits	Arboreal	B But is an arboreal feeder (Voth et al. 1980)	Terrestrial
External form	Tail long, more than half length of head and body	A	Tail short, less than half length of head and body
Ear	Small (10-12 mm); scantily haired	A (11-13 mm)	Large (13-16 mm); clothed with short straight hairs
Flank glands (Quay, 1968)	Absent	A	Present
Color of upper parts	Orange to red brown	A Rich brown	Brownish gray to plumbeous
Gastric mucous membrane pouch	Proximal flaps with long, irregular, deep serrations; distal rim with small, broad serrations	A	Proximal flaps with regular, short serrations; distal rim narrow, without serrations
Cecal villi	Delicate, unbranched	A A few branched	Robust, frequently branched
Anterior nasals viewed from above	Protrude well beyond anterior surface of incisors	A	Do not protrude beyond anterior surface of incisors
Length of diastema	6.7-7.5 mm	A (6.5-7.2 mm)	7.3-8.4 mm
Premaxilla-maxillary suture	Angle acute (ventrally about 25° to vertical axis of skull)	A	Angle less acute (ventrally about 70° to vertical axis of skull)
Width of palatine foramina	More than 1.5 mm	A	Less than 1.5 mm, frequently constricted posteriorly
Distance from root of incisor to nasal bone	Less than 2.05 mm, moderately smooth	A (1.6-1.8 mm)	More than 2.1 mm, indented
Distance between squamosals anteriorly	More than 7.7 mm	A	Less than 3.9 mm
Interparietal width	More than 7.7 mm	A	Less than 7.4 mm
Paraoccipital process	Close to bulla, not flaring posteriorly	A	Flaring posteriorly
Incisors (Howell, 1926)	More recurved	A	Less recurved
Third upper molar	Wide and short; posterior prism transversely placed and wide	A	Narrow and long; posterior prism long and narrow
Third lower molar	Wide and short	A (not so extreme)	Narrow and long

TABLE 1—(Continued)

Cervical vertebrae	More compressed antero-posteriorly	A (not so extreme)	Less compressed
Sacral foramina	Large	A	Small
Sternum	Wide	A (not as marked)	Narrow
Acromion process of scapula	Narrow	A	Wide
Hyoid bone	Medial spine absent or reduced; lateral processes short and nearly at right angles	A	Medial spine present and pronounced; lateral processes longer and flaring
Baculum	Separate medial osseous process absent; short lateral processes frequently fused	A	Well separated median and two lateral terminal processes (typical microtine)
Testes	Small; length x width less than 30 mm	A	Large; length x width more than 40 mm
Teats	Four	A 4, 5, and 6 recorded	Eight
Litter size	Two to three usual	A Two in one specimen; three in each of seven specimens; four in one specimen	Average 4.8 (2-8) (Foster 1961)
Karyotype, diploid number	52. In **A. longicaudus** "Quite different from **P. intermedius**" (Hsu, personal communication, 1968)	A 52. Compared to **A. longicaudus**, "similar but not identical" (Hsu, personal communication, 1971)	56

Literature Cited

Foster, J. B. 1961. Life history of the *Phenacomys vole*. J. Mammal. 42:181-198.

Howell, A. B. 1926. Voles of the genus *Phenacomys*. N. Amer. Fauna 48:1-66.

International Commission on Zoological Nomenclature. 1964. International Code of Zoological Nomenclature. London, England.

Johnson, M. L. 1973. Characters of the heather vole, *Phenacomys* and the red tree vole, *Arborimus*. J. Mammal. 54:239-244.

Maser, C., and M. L. Johnson. 1967. Notes on the white-footed vole (*Phenacomys albipes*). Murrelet 48:24-27.

———, and E. F. Hooven. 1969. A new locality record of *Phenacomys albipes*. Murrelet 50:22.

Merriam, C. H. 1901. Two new rodents from northwestern California. Proc. Biol. Soc. Washington 14:125-126.

Quay, W. B. 1968. The specialized posterolateral sebaceous glandular regions in microtine rodents. J. Mammal. 49:427-445.

Sherrell, P. E. 1970. A new locality record for *Phenacomys albipes*. Murrelet 50:39.

Taylor, W. P. 1915. Description of a new subgenus (*Arborimus*) of *Phenacomys*, with a contribution to knowledge of the habits and distribution of *Phenacomys longicaudus*, True. Proc. California Acad. Sci., Ser. 4, 5:111-161.

Voth, E. H., C. Maser, and M. L. Johnson. In press. Food habits of *Arborimus albipes*, the white-footed Vole. Northw. Sci.

Received March 17, 1980

Accepted for publication July 1, 1980

Robert E. Batie[1]

Department of Zoology
Oregon State University
Corvallis, Oregon 97331

Population Structure of the Crab Hemigrapsus oregonensis (Brachyura, Grapsidae) in Yaquina Bay Estuary, Oregon: I. Reproductive Cycle

Abstract

The *Hemigrapsus oregonensis* (Dana, 1851) population at Coquille Point in the Yaquina Bay Estuary was studied from April 1972 to May 1973. The population sex ratio slightly favored females (53.3 percent). The sex ratio did not change significantly with tidal height or season. The major reproductive season, as determined by the number of egg-bearing females, was from February to May (maximum brooding in March). Minimum brooding occurred during October. A regression model is presented for estimating fecundity.

Introduction

Hemigrapsus is a widely distributed genus of crab, occurring intertidally along the entire Pacific Rim from Alaska to Chile and in Japan, the USSR, China, Hawaii, and New Zealand. Although eleven species have been described within this genus, only two are found along the North American Pacific shores: *H. nudus* and *H. oregonensis*. Both range from Alaska to the Gulf of California (Schmitt, 1921; Hart, 1968). *H. nudus* is typically found in rocky outer coast areas with well-aerated, silt-free water. *H. oregonensis*, in contrast, is more common in regions with a higher silt load and, in general, is more typical of a muddy substratum (Way, 1917; MacKay, 1943). Hiatt (1948) has indicated that in those instances in which these two species overlap, there is usually a gradation of substrate types from a muddy or silty lower region, dominated by *H. oregonensis*, to a gravelly, well-drained upper region inhabited by *H. nudus*. At Coquille Point in the Yaquina Bay Estuary along the central Oregon coast, these two species are found in such an overlapping distribution.

Methods

The study area at Coquille Point in the Yaquina Bay Estuary (44° 37′ N. Lat., 124° 04′ W. Long.) was on the bay side of an abandoned artificial dike which had been constructed from dredge spoils. Small gravel, sandstone, and mudstone covered the dredge spoils. The substrate texture graded continuously from a fine, water-saturated mud at the 0 ft level to a pea-sized, well-drained gravel at the 5 ft level. Interspersed throughout the substrate were numerous shell fragments and large rocks measuring ½ ft-3 ft in diameter. The rocks were quite uniformly spaced from the 1 ft level to the 5 ft level, but at the 0 ft level the substrate consisted mainly of mud.

The study site was marked out in a grid from the 0 ft tidal level to the 5 ft tidal level at 1 ft vertical intervals. At each vertical foot interval, lines were extended hori-

[1]Present address: Department of Biology, Radford University, Radford, Virginia 24142.

zontally along the beach for 15 ft. A rod was placed to mark a subplot corner every 3 ft along the horizontal lines. Thus, the total sample area contained 25 subplots, with 5 at each tidal height. Each of the subplots had an area of about 3 m^2. Each month during the spring tidal cycle a complete population census was taken in one subplot at each tidal height. All crabs were hand-captured, sexed, determined if berried, measured, and returned to the same subplot from which they were captured. Sampling efficiency was estimated to be greater than 90 percent as fewer than 10 observed crabs per month escaped capture. Measurements of maximum carapace width were taken with an Almkvist excaliper and reported to the nearest one-hundredth of a centimeter.

Results and Discussion

The upper two tidal intervals (3-4 ft and 4-5 ft) supported the most crabs (716 and 713, respectively). The 1-2 ft tidal interval supported the fewest crabs (220). Although the majority of crabs were found in the upper regions, no apparent major seasonal vertical population shift occurred (Fig. 1). Non-seasonal movements did occur. In comparing the number of crabs present in the 3-4 ft interval from May 1972 to August 1972, large fluctuations were noted, suggesting a highly mobile adult population.

The frequency distribution of male and female crabs (Fig. 2) showed no size class differences between the sexes. The mean carapace width of females was, however, slightly less than for males (1.44 cm and 1.51 cm, respectively; $p < .05$). The percentage of females in monthly samples indicated that the sex ratio (53.3 percent females) was biased in favor of the females ($p < .01$). There did not appear to be any significant temporal variation about the mean sex ratio, indicating that the population sex ratio was fairly stable throughout the year. The percentage of females at each tidal height interval (Fig. 3) was more variable. The sex ratio appeared slightly biased in favor of females at the higher two tidal intervals. The percentage of females

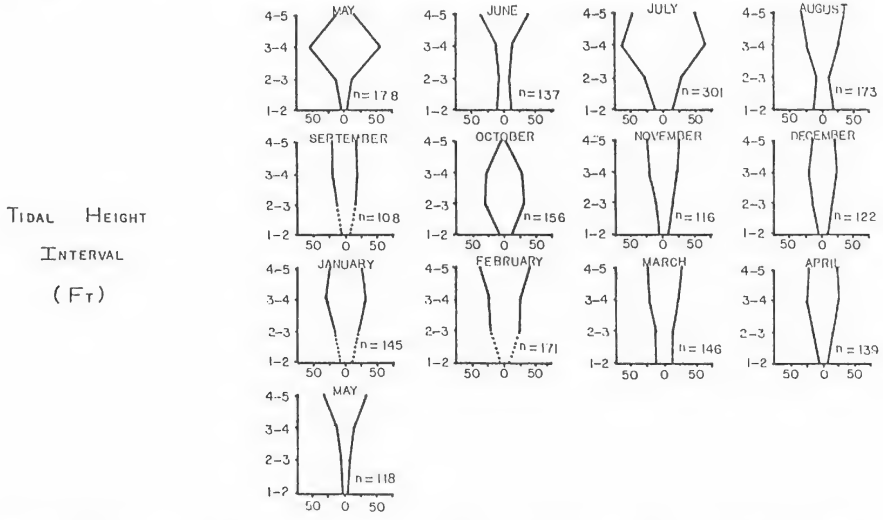


Figure 1. Total number of crabs collected monthly at each tidal height interval at Coquille Point in the Yaquina Bay Estuary, Oregon, from May 1972 through May 1973. Dotted lines indicate estimated numbers of crabs.

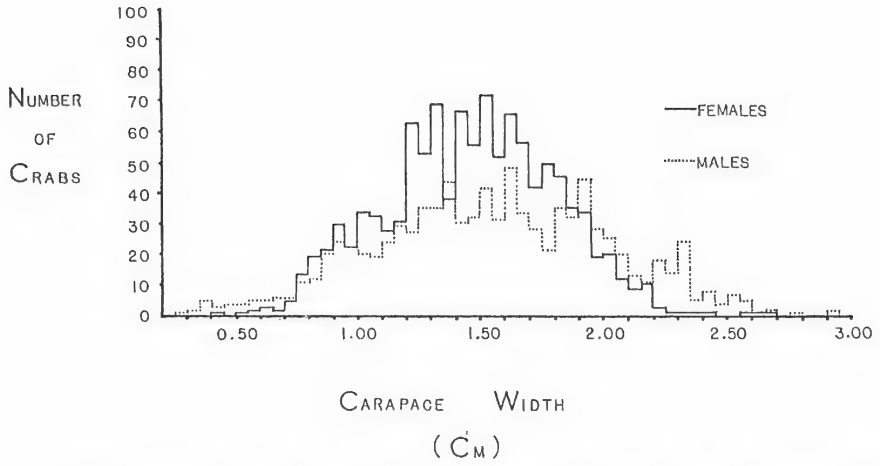


Figure 2. Histogram of number of male and female crabs in each carapace width size class during the period April 1972 through May 1973 at Coquille Point. Size class interval is 0.05 cm.

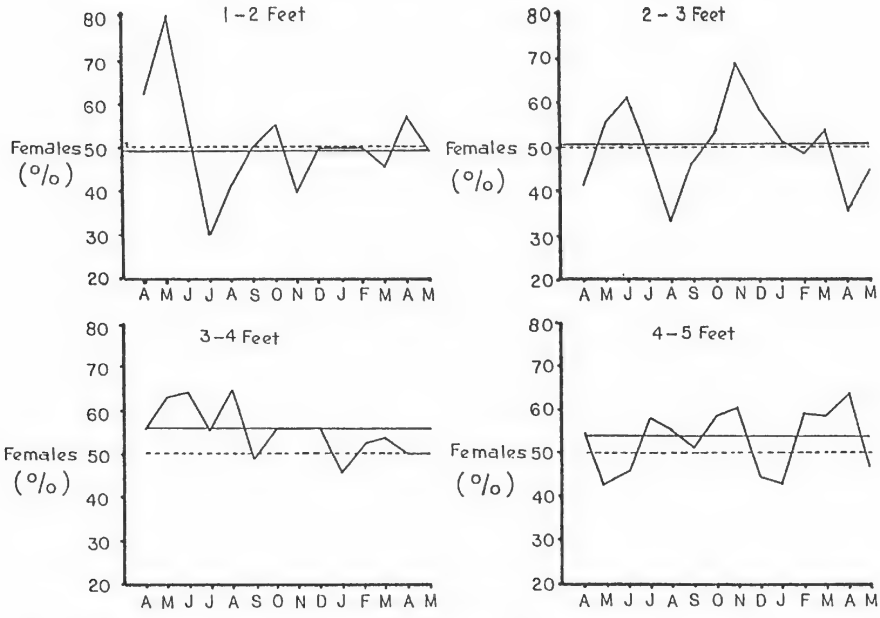


Figure 3. Percentage of female *Hemigrapsus oregonensis* in total population sample for each month at each tidal height interval. Solid line denotes average value from April 1972 through May 1973. Dashed line denotes hypothetical sex ratio (50 percent female).

from the 3-4 ft tidal interval appeared to decline throughout the study, and the percentage of females in the 4-5 ft interval appeared to increase (Fig. 3). Regression lines fitted to the data could not be shown to have a slope differing from zero ($p >$

.05), indicating a stable population sex ratio throughout the year at each tidal height interval.

The percentage of berried (ovigerous) females during the year (Fig. 4) showed a peak population reproductive effort during the late winter and spring months. The maximum percentage of berried females at any monthly interval (March 1973) was only about 33 percent of the female population. The minimum (1.4 percent) was during October. That some berried females were found each month indicated that the population was not synchronized for a major reproductive effort; rather, it exhibited a low-level, continuous yearly production which peaked in March. Fall months (September, October, November) were periods of little or no brooding at all tidal heights. The main reproductive period for this population was from February through May (maximum in March = 32.8 percent of females). The percentage of berried females at each tidal height reflected the population trend, indicating that there were no differences in reproductive seasons at the various tidal levels.

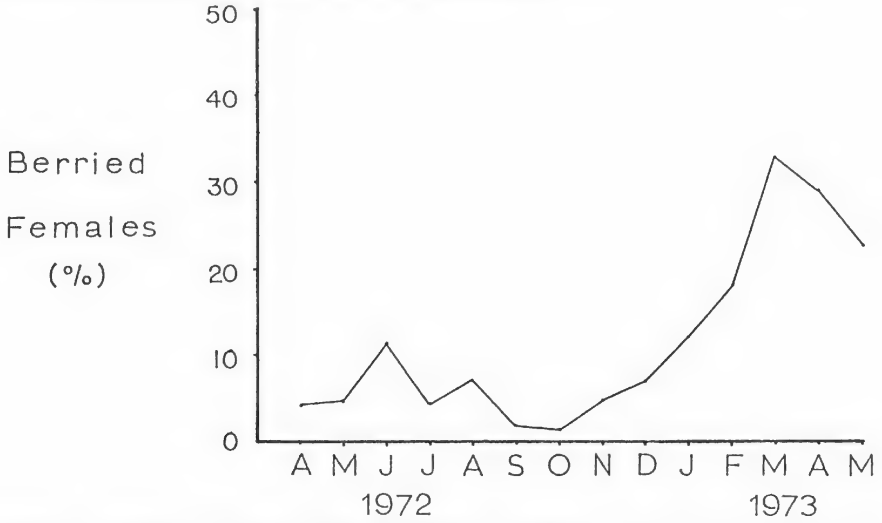


Figure 4. Percentage of berried female *Hemigrapsus oregonensis* at Coquille Point from April 1972 through May 1973. The minimum size of egg-bearing females was 0.86 cm. All female crabs smaller than this were not considered to be potentially reproductive female adults and were not included in the percentage calculations.

This is not the same brooding period that Knudsen (1964) found in Puget Sound, Washington, populations. He found that oogenesis occurred during a period of decreasing temperature (October to February). Increasing day length did not appear to regulate gametic production. Decreasing water temperature seemed to be a cue for early gametogenesis. However, a problem not resolved by Knudsen was the cue for the initiation of gametogenesis for a second brood class (70 percent of females). This second period of gametogenesis corresponded to rising water temperatures in Puget Sound. If Knudsen's assumptions are correct, then gametogenesis occurred twice yearly in the Puget Sound population, once in the fall and winter on a decreasing temperature cycle and again in late winter and spring on a rising temperature cycle.

Kuris (1971, 1978) reported that maximum brooding in *H. oregonensis* from

Bodega Bay, California, occurred from November through February (first brooding period: 65 percent of females) and from June through August (second brooding period: 43 percent of females). Summer brooding occurred in both California and Washington populations. In Puget Sound, however, no winter brooding occurred. Egg deposition first occurred in February, rapidly increased in March, and peaked in May (first brooding period: 90 percent of females). A second brooding period (70 percent of females) occurred during August. The Yaquina Bay population had a single maximum brooding period (March) which corresponded with neither the Bodega Bay nor the Puget Sound populations.

In Yaquina Bay, surface water temperature increased from December to April. A large drop in temperature (13° to 8° C) occurred from September to December. These findings suggested that decreasing temperature in the fall may also be a cue for gametogenesis in Yaquina Bay crabs just as Knudsen found decreasing water temperature to be a cue in Puget Sound populations. The results showed that in Yaquina Bay only about 33 percent of the females of reproductive size (0.86 cm and larger) were gravid at any one time. In addition, only one major brood occurred during the year. These data suggest that the bay population was either a) not well synchronized as a population for one short period of maximal reproductive effort per year, b) not well adapted to the environmental challenges of the bay, or c) both. In the Yaquina Bay Estuary, the salinity regime does not remain as stable as it does in Puget Sound or along the outer coast areas. After large rains on the Yaquina Bay watershed, freshwater runoff may lower the salinity to near 0-5 $^{o}/_{oo}$. Although *H. oregonensis* is euryhaline and can tolerate 0 $^{o}/_{oo}$ (tap water) for 20 h (Low, 1970), nothing is known about the effects of low salinity influx on gametogenesis. It is suspected, however, that low salinity or fluctuating salinity during periods of gametogenesis or brooding adversely affects reproductive success. In other habitats to the south and north of Yaquina Bay, brooding percentages are nearly 100 percent (Boolootian *et al.*, 1959; Knudsen, 1964). I suspect, therefore, that Yaquina Bay is a marginal habitat for *H. oregonensis* in which maximum reproduction does not occur.

A measure of female fecundity was established by regressing carapace width of brooding females with the number of eggs brooded for females in various size classes. A linear relationship ($r = 0.9018$) was established for females from 1.04 to 2.03 cm in carapace width. A regression model was established from which the number of brooded eggs could be estimated if a female's carapace width were known. The model is:

Y (number of eggs brooded) =
$r = 0.9018$
$-1.0529 \times 10^4 + (1.3344 \times 10^4)$ (carapace with in cm)
t-value
constant = −5.6813
variable coefficient = 10.4351

An estimate of the average egg production per female was about 10,000 eggs/female per year (assuming a single brooding cycle per female per year). Thus, an average of about 270,000 eggs/m^2 were produced at the collection site each year. Since it appeared that there was a large population turnover each year and since there was a fairly stable adult population, it was estimated that for about every 5000 eggs produced, one would survive to become an adult. The adjusted egg mortality rate to maintain a

stable population was estimated to be 99.98 percent. Fecundity of the average (1.44 cm) female crab did not vary greatly from similar sized crabs from Bodega Bay (about 8000 eggs/brood) (Kuris, 1971). A smaller percentage of females reproduce in Yaquina Bay than in Bodega Bay. Those few females that do reproduce in Yaquina Bay appear to produce the same brood size per crab as in Bodega Bay.

Total densities of population vary dramatically. Outer coast populations have densities of up to 500/m^2 (Low, 1970). The maximum density found in Yaquina Bay was about 20 crabs/m^2, indicating that Yaquina Bay may be a marginal habitat not only for reproductive success but also in supporting large numbers of adults.

Summary and Conclusions

The *Hemigrapsus oregonensis* population at Coquille Point in the Yaquina Bay Estuary was vertically stratified. The 1-2 ft vertical interval had an average of 7.89 crabs/m^2, the 2-3 ft interval 11.84 crabs/m^2, the 3-4 ft interval 20.9 crabs/m^2, and the 4-5 ft interval 19.73 crabs/m^2. Carapace width versus frequency histograms indicated no obvious size classes. Average female carapace width (1.44 cm) was slightly smaller than average male carapace width (1.51 cm). The population sex ratio was slightly biased in favor of females (53.3 percent). No obvious segregation of sexes occurred by tidal height during the study. Brooding females were found each month during the study. The main reproductive period was February through May (maximum in March = 32.8 percent). September through December was the period of fewest gravid females. The percentage of berried females at each tidal height followed the same trend: fall minimum brooding and spring maximum brooding. The minimum size of reproducing females was found to be 0.86 cm carapace width. A regression equation between carapace width and number of brooded eggs was established as a measure of fecundity:

$$Y(\#\text{brooded eggs}) = -1.0529 \times 10^4 + (1.3344 \times 10^4)(\text{carapace width in cm}).$$

Acknowledgments

I thank Dr. C. J. Bayne, Department of Zoology, Oregon State University, Corvallis, Oregon, for his help and guidance during this study. I also thank the Department of Zoology, Oregon State University, for providing the support which made this study possible. I extend special thanks to the Chesapeake Bay Center for Environmental Studies (Smithsonian Institution), Edgewater, Maryland, for providing space, guidance, and resources during the preparation of this manuscript.

Literature Cited

Boolootian, R. A., A. C. Giese, A. Farmanfarmaian, and J. Tucker. 1959. Reproductive cycles of five west coast crabs. Physiol. Zool. 32:213-220.

Hart, J. F. L. 1968. Crab-like Anomura and Brachyura (Crustacea: Decapoda) from southeastern Alaska and Prince William Sound. Nat. Hist. Pap. Natn. Mus. Can. 38:1-6.

Hiatt, R. W. 1948. The biology of the lined crab *Pachygrapsus crassipes* Randall. Pac. Sci. 2:134-213.

Knudsen, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crab-like Anomura of Puget Sound, Washington. Pac. Sci. 18:3-33.

Kuris, A. M. 1971. Population Interactions between a Shore Crab and Two Symbionts. Berkeley, Univ. of California Ph.D. thesis.

———. 1978. Life cycle, distribution and abundance of *Carcinonemertes spialti*, a nemertean egg predator of the shore crab, *Hemigrapsus oregonensis*, in relation to host size, reproduction and molt cycle. Biol. Bull. 154:121-137.

Low, C. J. 1970. Factors Affecting the Distribution and Abundance of Two Species of Beach Crabs, *Hemigrapsus oregonensis* and *H. nudus*. Univ. of British Columbia, Vancouver, M.A. thesis.
MacKay, D. C. G. 1943. The brachyuran crabs of Boundary Bay, British Columbia. Can. Field. Nat. 57(9):147-152.
Schmitt, W. L. 1921. The Marine Decapod Crustacea of California. Univ. Calif. Publ. Zool. 23.
Way, E. 1917. Brachyura and crab-like Anomura of Friday Harbor, Washington. Puget Sound Mar. Sta. Publ. 1:349-382.

Received April 15, 1980
Accepted for publication August 15, 1980

J. D. Helvey

Northeastern Forest Experiment Station
Timber and Watershed Laboratory
Parsons, West Virginia 26287

and

W. B. Fowler

Pacific Northwest Forest and Range Experiment Station
Forest Hydrology Laboratory
Wenatchee, Washington 98801

Precipitation Variability in the Columbia Basin of Washington

Abstract

This paper describes time and space variability of precipitation in the semiarid climate of the Columbia Basin in Washington State. Annual variation, as indicated by the coefficient of variation, averages 24.47 percent for the 19 stations used in the analysis. Variation is greater during spring and summer months than during fall and winter. Average annual precipitation increases about 2.47 cm for each 100 m increase in elevation. Simple correlation of annual or seasonal precipitation decreases rapidly as distance between stations increases.

Introduction

Climate of the Columbia Basin in Washington State is classified as semiarid because potential evaporation during each year exceeds annual precipitation amounts (Trewartha, 1943). Precipitation usually occurs in the form of general cyclonic storms during the winter months and thunderstorms during the warm months. Because thunderstorm cells usually cover a limited land surface area, variation in amounts of rainfall between measuring sites is usually very large. In fact, extreme variability of precipitation from year to year and from point to point within a given year is one characteristic of semiarid zones (Trewartha, 1943). The objective of this research was to use historical precipitation records to describe the variation in annual precipitation amounts from year to year at individual sites, and from site to site within individual years.

Study Area

The Columba Basin is located in the east-central part of Washington State. Prevailing winds are from west to east; thus, a major rain shadow is created by the Cascade Range, which is oriented north-south, roughly parallel to the Pacific Ocean and located just west of the Columbia Basin. Figure 1 shows the location of the study area and the precipitation stations which were used in this analysis. The stations vary in elevation from 169 m at Trinidad to 798 m at Waterville. Conclusions drawn here are directly applicable only to the area represented by the stations identified in Figure 1. However, comparison of these results with results from other semiarid areas may indicate more general application.

Precipitation records in the Columbia Basin began in the latter part of the nineteenth century. In 1900, there were 27 reporting stations in eastern Washington. During this

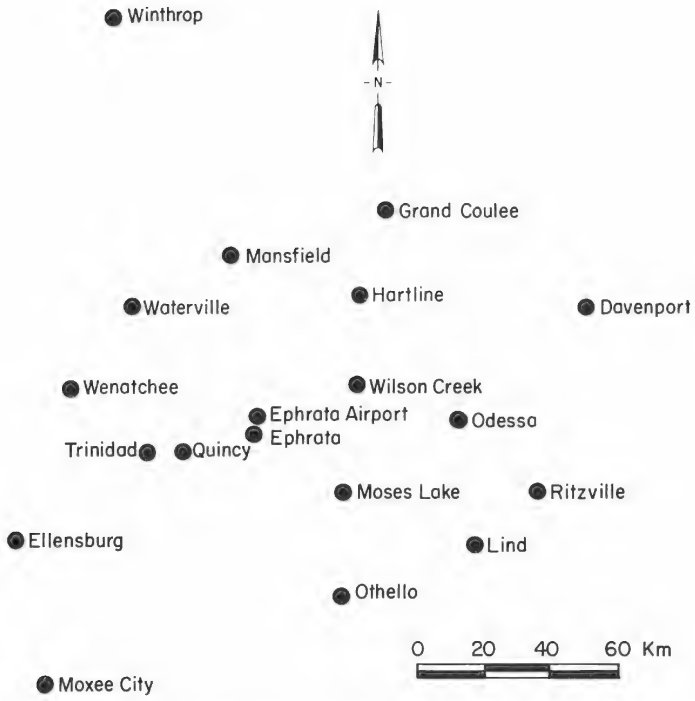


Figure 1. Relative location of the climatic station used in the analysis.

century, several new stations were started, operated a few years, and then discontinued. Also, some original stations were closed when volunteer operators moved away. Even today, the rain gauge density is extremely sparse with an average of only one gauge per 971 sq km, or an average distance of 30.4 km between gauges. In some areas, rain gauges are more than 50 km apart.

Previous Work

The magnitude of the correlation of precipitation or temperature measured at two stations depends on the distance between the stations. As distance between the stations increases, correlations usually decrease. Godshall (1977) computed the correlation of air temperature between stations as much as 1610 km apart. His highest correlation was about 0.8 between stations which were no more than 80 km apart. As distance increased between the reference and test stations, correlations decreased logarithmically; at 1280 km, the values had declined to about 0.2. The same general relationships were presented by Longley (1974) for precipitation data in the prairie provinces of Canada. Longley was able to plot general storm tracks during the summer months based on his correlation analysis.

Methods

Data published by the U.S. Weather Bureau were used to determine precipitation

variability. The data are summarized by season (August-February and March-July) and water year (August-July). The water year is started on 1 August because August usually is the driest month of the year. Also, it represents the approximate date when the native vegetation, big sagebrush (*Artemisia tridentata* Nutt.), stops growing.

Analyses of each season were made in which the correlations of annual precipitation between a selected base station and each of the other stations listed in Figure 1 were computed. Next, the distance between the base station and each of the other stations was measured on a map. A graph was plotted in which the correlation coefficient between stations was the dependent variable and distance between the same stations was the independent variable.

Results and Discussion

Tables 1, 2, and 3 contain statistics on annual, spring-summer, and fall-winter precipitation, respectively (including averages, standard deviations, coefficients of variation, as well as the record length and elevation of each station used in this study). Periods of record vary from 27 to 45 years, and annual averages vary from 19.3 cm at the Ephrata Airport to 36.7 cm at Winthrop. Although the elevation range is limited, there is a slight increase in average annual precipitation with elevation (Fig. 2).

The regression of average annual precipitation on elevation was determined as follows:

$$\text{Precipitation (cm)} = 13.25 + 0.247 \text{ (elevation, m)}$$

This function, which has a coefficient of determination (r^2) of 0.47, indicates that average annual precipitation increases 2.47 cm for each 100 m increase in elevation. The regression is significant ($P \leq 0.01$).

Plottings were made of correlation coefficient (r) and distance between pairs of climatic stations. In general, the relationship presented in Figure 3, in which Wenatchee

TABLE 1. Average annual precipitation (1 August-31 July) and its variation between years.

Station	Elevation (m)	Precipitation			Years of record
		average (cm)	standard deviation (cm)	coefficient of variation (percent)	
Davenport	750	40.9	8.8	22	43
Ellensburg	463	22.8	5.6	24	40
Ephrata	389	20.3	5.5	27	43
Ephrata Airport	384	19.3	4.7	24	27
Grand Coulee	518	26.6	6.6	25	41
Hartline	582	27.0	6.5	24	27
Lind	497	23.3	4.9	21	28
Mansfield	690	26.9	5.0	21	27
Moses Lake	368	19.5	4.6	23	27
Moxee City	472	19.8	5.8	29	28
Odessa	469	26.0	7.0	27	45
Othello	363	20.2	6.1	30	27
Quincy	388	20.5	5.5	28	27
Ritzville	558	28.4	5.9	20	27
Trinidad	169	21.0	5.6	27	29
Waterville	799	28.9	6.8	24	45
Wenatchee	193	22.8	5.5	24	45
Wilson Creek	389	22.4	4.9	22	28
Winthrop	535	36.7	8.4	23	44

TABLE 2. Average precipitation between 1 August and 1 March and its variation between years.

Station	Precipitation		
	average (cm)	standard deviation (cm)	coefficient of variation (percent)
Davenport	26.6	6.1	23
Ellensburg	15.5	4.0	26
Eprata Airport	12.7	3.6	28
Ephrata	13.1	3.8	29
Grand Coulee	16.4	4.2	26
Hartline	17.8	5.1	29
Lind	15.5	4.5	29
Mansfield	17.9	4.9	28
Moses Lake	12.8	3.4	27
Moxee City	12.6	4.0	32
Odessa	16.5	4.2	26
Othello	13.6	5.5	40
Quincy	13.4	4.0	30
Ritzville	19.1	5.2	27
Trinidad	13.4	3.8	29
Waterville	19.1	5.7	30
Wenatchee	16.0	4.4	28
Wilson Creek	14.9	4.0	27
Winthrop	26.5	7.5	28

TABLE 3. Average precipitation between 1 March and 1 August and its variation between years.

Station	Precipitation		
	average (cm)	standard deviation (cm)	coefficient of variation (percent)
Davenport	14.3	5.9	41
Ellensburg	7.3	3.8	52
Ephrata Airport	6.6	3.1	48
Ephrata	7.2	3.7	51
Grand Coulee	10.2	5.1	50
Hartline	9.2	3.6	40
Lind	7.8	2.0	26
Mansfield	9.0	3.7	41
Moses Lake	6.7	2.1	31
Moxee City	7.2	3.5	48
Odessa	9.5	5.0	52
Othello	6.6	2.7	41
Quincy	7.1	3.5	49
Ritzville	9.3	3.0	32
Trinidad	7.6	4.5	59
Waterville	9.8	5.3	54
Wenatchee	6.8	4.3	43
Wilson Creek	7.5	3.0	40
Winthrop	10.2	4.7	46

and Ephrata are used in turn as the base stations, is typical. Although the graph indicates the expected inverse relationship between correlation and distance, the logarithmic relationship presented by Longley (1974) is not evident. One reason for this lack may be the limited distance between stations in the Columbia Basin. Longley's maximum distance between stations was 1200 km, compared to the maximum of only 200 km in this study.

Another way to present correlation data is to select a base station near the center

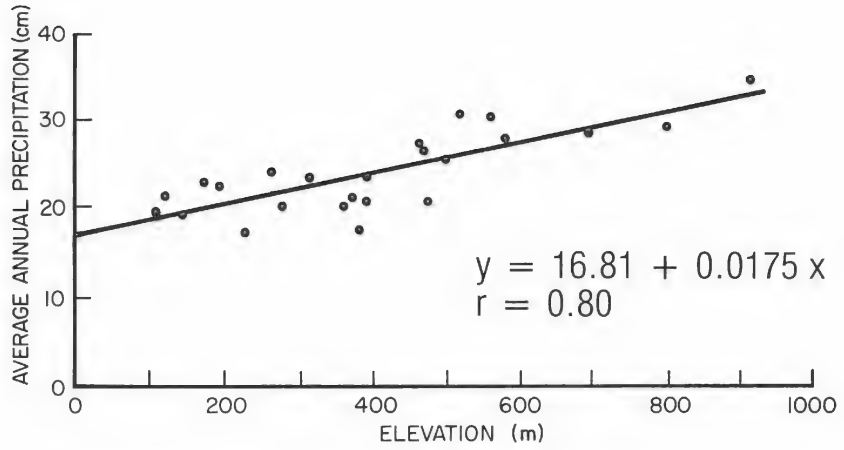


Figure 2. Relationship between elevation and average annual precipitation.

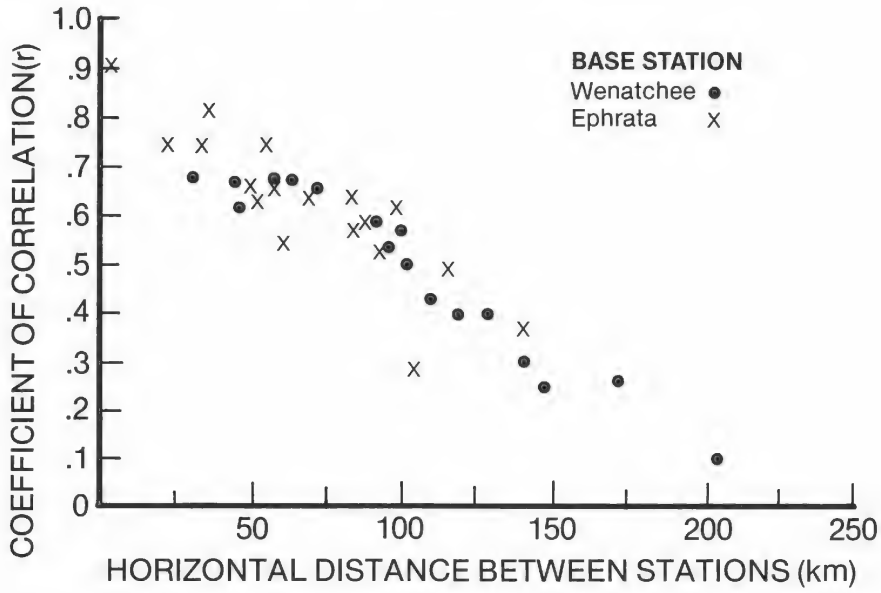


Figure 3. Relationship between correlation of annual precipitation (August-July) and distance between stations. Wenatchee and Ephrata are used in turn as the base stations.

of the study area and draw lines of approximately equal correlation based on data from surrounding stations. Figure 4 uses Ephrata as the base station. This figure illustrates the reliability of estimating annual precipitation at an ungauged site from records collected some distance away. Correlation at 32 km is about 0.7; at 64 km it drops to about 0.6. Figure 4 clearly illustrates the uncertainty in using records from an estab-

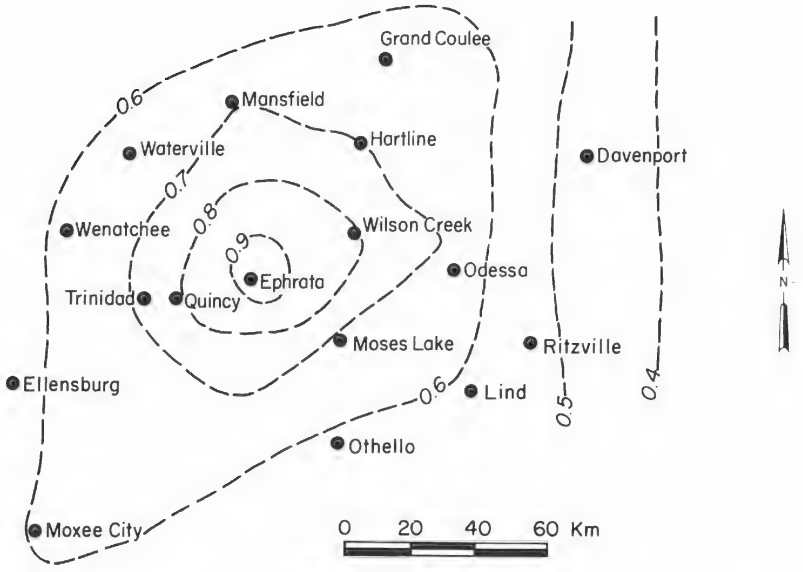


Figure 4. Lines of approximate equal correlation between annual precipitation measured at Ephrata and the other climatic stations in the Columbia Basin.

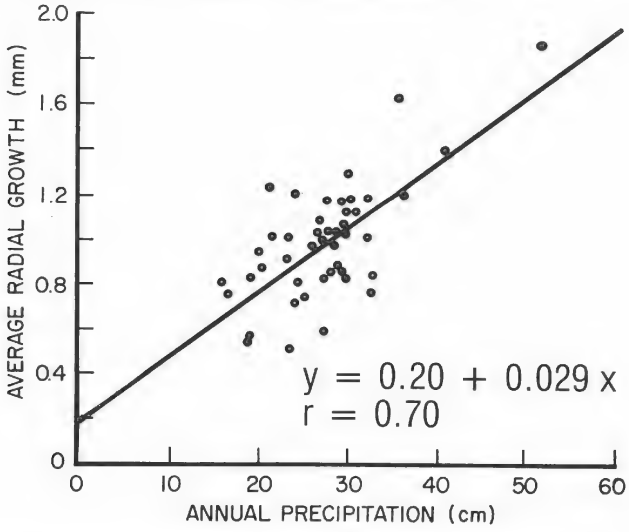


Figure 5. Relationship between average annual radial growth of sagebrush growing at Steamboat Rocks and measured annual precipitation at Mansfield.

lished climatic station to estimate annual precipitation at ungauged sites more than a few kilometers away.

We (Fowler and Helvey, 1974) reasoned that native plants growing at remote sites would provide an alternative way to estimate annual precipitation at those sites during past years. Although our preliminary results (Fig. 5) are encouraging, more testing is needed before a model can be developed to predict rainfall amounts from annual radial increments of sagebrush growth. Variables needed to be evaluated, in addition to precipitation, include the following: elevation, soil fertility, and land use history (i.e., fire, grazing, and so forth). Until such models are developed, or the rain-gauge networks expanded, estimates of annual or seasonal precipitation at points several kilometers away from established gauges will not be precise.

Literature Cited

Fowler, W. B., and J. D. Helvey. 1974. Effect of large-scale irrigation on climate in the Columbia Basin. Science 184:121-127.

Godshall, Fredric A. 1977. The statistical structure of surface temperature fields. Monthly Weather Review 103(7):523-526.

Longley, Richmond W. 1974. Spatial variation of precipitation over the Canadian prairies. Monthly Weather Review 102(4):307-312.

Trewartha, Glenn T. 1943. An Introduction to Climate. McGraw-Hill Book Company, Inc., New York and London.

Received April 5, 1980
Accepted for publication December 24, 1980

T. E. Owens[1]

Department of Wildlife
College of Forestry, Wildlife and
Range Sciences
University of Idaho
Moscow, Idaho 83843

Postburn Regrowth of Shrubs Related to Canopy Mortality

Abstract

An experimental fall burn was conducted in a northern Idaho seral shrub field on a Douglas-fir/ninebark habitat type. Production of current annual twig growth (CAG) of redstem ceanothus, oceanspray, ninebark, and Scouler willow was correlated with the amount of canopy mortality following burning. Postburn shrub productivity, measured as lengths and weights of CAG, was found to increase directly with the degree of canopy mortality.

Introduction

Knowledge of shrub response to different intensities of fire is needed to assess effects of burning for wildlife habitat improvement. DeWitt and Derby (1955) stated that the duration of the increased nutritive quality of browse caused by burning was directly related to burn intensity, but they failed to discuss the mechanism by which this result came about. This paper describes the regrowth response of four shrub species—redstem ceanothus (*Ceanothus sanguineus*), oceanspray (*Holodiscus discolor*), ninebark (*Physocarpus malvaceus*), and Scouler willow (*Salix scouleriana*) (Hitchcock and Cronquist, 1973)—to different degrees of fire-induced canopy mortality.

Study Area

The study area was a 16 ha prescribed burn on a 30° south exposed slope in the Douglas-fir/ninebark (*Pseudotsuga menziesii/Physocarpus malvaceus*) habitat type (Daubenmire and Daubenmire, 1968). The burn was located on Basalt Hill within the 324 ha Hatter Creek enclosure of the University of Idaho Experimental Forest, six miles south of Princeton, Latah County, Idaho. The burn area encompassed two cover types: an upland midshrub type in which ninebark and snowberry (*Symphoricarpos albus*) predominated, and a more mesic tall shrub complex in which Scouler willow was dominant. Redstem ceanothus, oceanspray, birchleaf spirea (*Spiraea betulifolia*), baldhip rose (*Rosa gymnocarpa*), and Oregon grape (*Berberis repens*) were found interspersed among these two types in varying densities.

Methods

Prior to the burn, 50 samples of current annual twig growth (CAG) of redstem, oceanspray, ninebark, and willow were clipped in the fall from each of the cover types,

[1]Current address: Washington State Department of Game, Nongame Program, c/o The Evergreen State College, 3109 Seminar Building, TA-00, Olympia, Washington 98505.

measured for length, and weighed after oven drying. The study area was burned on 17 October 1977 when temperature was 23°C, relative humidity 27 percent, and winds 0-5 km/h from the west. The patchy head fire of moderate intensity attained flame heights of 2-100 cm. To determine the effect of differential canopy mortality on productivity of shrub regrowth for each type, at least four individual ninebark, oceanspray, redstem, and willow plants were assigned to one of four mortality classes: 1 = 0 percent; 2 = 1-50 percent; 3 = 51-99 percent; 4 = 100 percent canopy mortality. A minimum of 16 individuals per species per shrub cover type were sampled for CAG productivity. Where possible, at least 20 samples of CAG were clipped, measured, and weighed from each individual shrub. A total of 153 shrubs were assigned to postburn mortality classes, and a total of 3032 twigs were clipped, measured, and weighed.

Canopy Mortality and CAG Response

Analysis of variance and Duncan's multiple range tests of CAG length and weight by mortality class demonstrated that the degree of canopy mortality directly influenced shrub CAG production (Table 1). All four species displayed greater CAG length and weights in shrubs having greater than 50 percent mortality than shrubs subjected to less than 50 percent canopy mortality (Fig. 1). Regrowth response of redstem, ninebark, and willow, whose canopies were completely killed by fire, was more vigorous than that of shrubs whose canopies were only partially killed. Ninebark CAG weights

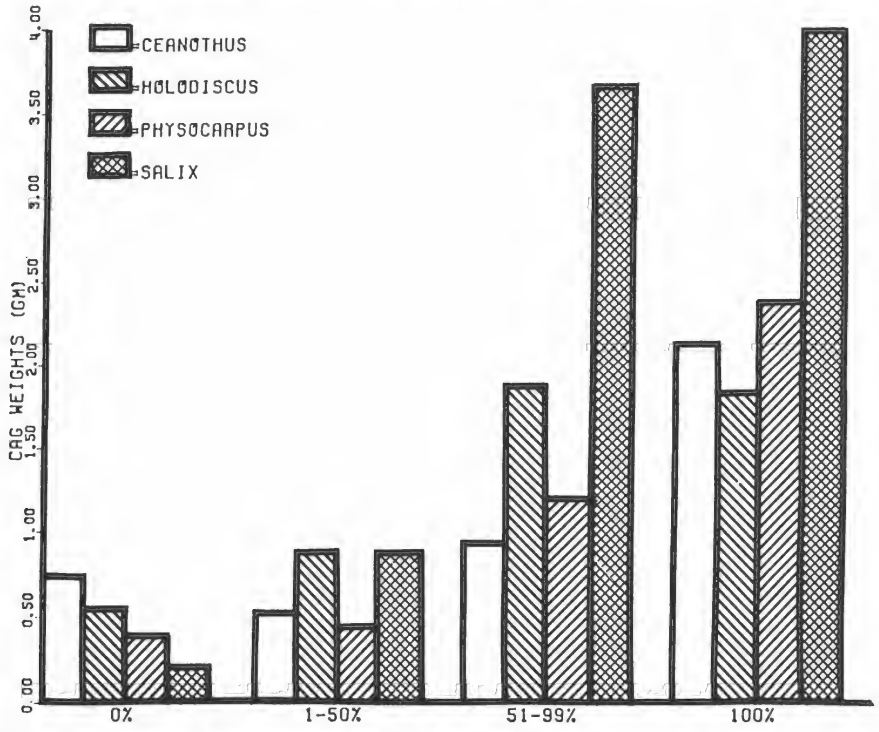


Figure 1. Twig weight relationships to canopy mortality classes.

TABLE 1. Twig weight and length relationships to canopy mortality classes as determined by Duncan's multiple range test. Canopy mortality classes are: 0 = preburn; 1 = 0 percent; 2 = 0-50 percent; 3 = 51-99 percent; 4 = 100 percent burned. Postburn means with same letters are not significantly different ($\alpha = .05$).

		MIDSHRUB					TALL SHRUB					TOTALS				
		Twig length			Twig weight		Twig length			Twig weight		Twig length			Twig weight	
Species	Mortality Class No.	$\bar{x}$(mm)	Grouping	Sample Size	$\bar{x}$(gm)	Grouping	$\bar{x}$(mm)	Grouping	Sample Size	$\bar{x}$(mm)	Grouping	$\bar{x}$(mm)	Grouping	Sample Size	$\bar{x}$(gm)	Grouping
Redstem	0	9		50	0.09		6		50	0.04		7		100	0.07	
	1	18	C	115	0.72	C	22	B	64	0.78	B	19	B,C	179	0.74	B,C
	2	14	C	129	0.40	D	23	B	83	0.82	B	17	C	233	0.53	C
	3	26	B	70	1.22	B	19	B	66	0.67	B	23	B	136	0.95	B
	4	42	A	68	1.70	A	62	A	53	2.72	A	51	A	121	2.15	A
Oceanspray	0	10		50	0.08		12		50	0.14		11		100	0.11	
	1	22	B	72	0.56	B	20	C	74	0.46	B	21	B	146	0.51	C
	2	19	B	205	0.64	B	45	B	51	2.20	A	24	B	276	0.93	B
	3	30	A	89	1.18	A	65	A	86	2.70	A	47	A	175	1.93	A
	4	32	A	84	1.58	A	68	A	57	2.88	A	43	A	161	1.87	A
Ninebark	0	9		50	0.12		11		50	0.12		10		100	0.12	
	1	10	C	72	0.27	C	16	C	77	0.57	B	13	C	149	0.42	C
	2	12	C	169	0.47	C	12	C	21	0.30	B	12	C	190	0.45	C
	3	26	B	85	1.42	B	25	B	76	0.93	B	25	B	161	1.18	B
	4	52	A	72	2.81	A	44	A	71	2.03	A	48	A	143	2.42	A
Willow	0	8		50	0.05		16		50	0.20		12		100	0.12	
	1	16	C	109	0.24	C	10	C	85	0.16	C	13	D	194	0.20	C
	2	37	B	65	1.40	B	22	C	84	0.56	C	29	C	149	0.93	B
	3	68	A	47	2.50	A	83	B	60	4.61	B	76	B	107	3.68	A
	4	71	A	85	2.99	A	168	A	27	7.07	A	94	A	112	3.98	A

and willow CAG length and weights demonstrated this relationship well, as these measures of productivity increased directly with the degree of canopy mortality. The CAG lengths of ninebark and the lengths and weights of redstem followed a similar pattern, but in these species, unburned shrubs were more productive than those with less than 50 percent canopy mortality. Only the oceanspray data indicated superior productivity at the level of greater than 50 percent canopy mortality as opposed to the 100 percent mortality class.

Mean lengths and weights of CAG were generally greater for those shrubs in the more mesic tall shrub type (Table 2). An exception to this trend was ninebark. Ninebark regrowth in the midshrub and tall shrub types was not significantly different for mortality classes 2 and 3; for mortality classes 3 and 4, the regrowth of ninebark was actually greater for the drier site. All species measured had significantly greater ($\alpha = .05$) CAG lengths and weights after the fire except willow (Table 3).

Discussion

The different response of redstem and oceanspray may have been due to specific differences in burn tolerance. The superior productivity of redstem's unburned plants over lightly burned plants have indicated that low levels of canopy mortality may not have caused sufficient damage to the plant to simulate vigorous basal sprouting, yet the canopy may have been sufficiently damaged to decrease CAG productivity. The superior productivity of oceanspray in mortality class 3 over mortality class 4 may have been caused by inadvertent sampling of plants which burn so intensely as to sustain root crown damage, or these results may indicate lower fire tolerance.

The response variability was obscured when data from both transects were combined (Table 1). The same trends as previously discussed were still evident. Differentiation among mortality classes was more distinct for all shrubs in the midshrub type, the more xeric site. The higher soil moisture of the tall shrub type allowed for greater response for all mortality classes, obscuring some of the partial canopy mortality effects. In the more xeric sites, the limited soil moisture may have curtailed the vigor of post-

TABLE 2. Relationship of twig lengths and weights of regrowth of four species in two cover types related to mortality class following burning, as determined by an unpaired t-test; a = significantly different at $\alpha = .01$; b at $\alpha = .05$; c at $\alpha = .10$; and NS = no significant difference between cover types.

Species	Mortality class no.	Mean twig lengths (mm)			Mean twig weights (gm)		
		Midshrub	Tall shrub	t-test	Midshrub	Tall shrub	t-test
Redstem	1	17.9	22.1	b	0.72	0.78	NS
	2	14.3	22.5	a	0.40	0.82	a
	3	26.4	18.9	b	1.21	0.64	b
	4	41.5	62.4	a	1.70	2.71	a
Oceanspray	1	22.3	19.6	b	0.58	0.45	NS
	2	18.8	44.6	a	0.63	2.20	a
	3	30.0	65.0	a	1.18	2.70	a
	4	32.0	68.0	a	1.57	2.87	a
Ninebark	1	10.0	16.0	a	0.26	0.57	c
	2	11.7	12.0	NS	0.46	0.30	NS
	3	26.0	24.8	NS	1.42	0.91	NS
	4	51.6	44.3	c	2.80	2.03	c
Willow	1	15.7	9.8	a	0.23	0.16	a
	2	37.0	22.0	a	1.40	0.56	c
	3	68.0	83.0	NS	2.50	4.60	b
	4	71.0	168.0	a	2.99	7.07	a

TABLE 3. Mean lengths and weights of current-annual-growth of four shrubs in two cover types for two years. a = Means significantly different from midshrub ($\alpha = .01$); b = Means of mid- and tall shrub types not significantly different; c = Means significantly different from preburn means ($\alpha = .01$); d = Means not significantly different from preburn means.

	Preburn Midshrub			Preburn Tall shrub			Preburn Both types			Postburn No canopy mortality		
Species	Length	Weight	N	Length	Weight	N	Length	Weight	N	Length	Weight	N
Redstem	8.6	0.09	50	5.7[a]	0.04[a]	50	7.13	0.07	100	19.43[c]	0.74[c]	179
Oceanspray	9.7	0.08	50	12.2[a]	0.14[a]	50	10.93	0.11	100	20.95[c]	0.52[c]	146
Ninebark	8.8	0.12	50	10.7[a]	0.12[b]	50	9.78	0.12	100	13.31[c]	0.42[c]	149
Willow	8.0	0.05	50	15.7[a]	0.20[a]	50	11.87	0.12	100	13.12[d]	0.20[c]	194

burn resprouting, especially when canopies were partially damaged. The remaining canopy may have competed for the limited soil moisture, thereby decreasing basal sprout CAG. This trend was further illustrated by a series of unpaired t-tests between sites performed for each mortality class by species (Table 2).

Daubenmire and Daubenmire (1968) suggested that ninebark may be adapted to more xeric sites than oceanspray, redstem, and willow. Mueggler's (1965) shrub species association analysis also demonstrated ecological dissimilarities among ninebark, redstem, and willow. This difference in tolerance of xeric conditions might have best expressed itself after ninebark was stressed by fire-induced canopy kill. These differences in CAG response (lengths and weights) between transects for all species studied tended to obscure the mortality class-CAG response relationships.

T-tests between preburn and postburn mortality class 1 (unburned) CAG lengths and weights for each species indicated that CAG productivity of unburned plants was greater after the fire (Table 3). Some fire induced factors included soil infiltration (Tarrant, 1956; Biswell and Schultz, 1957), greater macronutrient availability (Isaac, 1963; Shearer, 1976; Bollen, 1974), and higher temperatures (Fowells and Stephenson, 1934). Fire independent factors included climatic differences between years.

The growing season in 1978 was more moist than in 1977. The previous 12 months' precipitation (October-September) influencing the CAG for 1977 and 1978 was 42.0 and 75.1 cm, respectively (U.S. Dept. of Commerce, 1976-1978). Thirty-three cm more precipitation were available during the 12 months preceding the postburn shrub data acquisition than were available during the 12 months preceding the preburn shrub data collection. This difference in moisture regimes may have been more influential in creating the CAG length and weight differences of unburned shrubs than were the fire-induced factors previously discussed. While such precipitation differences may have accounted for most, if not all, pre- and postburn differences in unburned shrub production, the comparisons between canopy mortality classes after the fire are not influenced.

CAG of young, vigorously growing plants is more nutritious than that of mature, slow growing plants (Short *et al.*, 1972). The increased postburn nutritive value is probably due to increased macronutrient and soil moisture availability and the vigorous regrowth response stimulated by canopy mortality. The data presented in this study suggest a possible explanation of DeWitt and Derby's (1955) fire intensity/browse quality endurance relationship. These data demonstrate that postburn shrub productivity is directly related to the degree of canopy mortality, which is a function of fire intensity. Plants that experience severe canopy mortality concentrate their nutrients into vigorous regrowth more than shrubs which suffer only light canopy mortality.

In this study, some lightly burned canopies were actually less productive than unburned canopies. In most species, productivity was highest where canopy mortality was greatest. The increased vigor of this regrowth is shortlived and tapers off 3 to 10 years postburn; any increased vigor noted in lightly burned plants often endures for the first postburn growing season only (Cooperrider and Behrend, 1980; Mueggler, 1965; Neuenschwander *et al.*, 1978). The longer lasting increased nutritive value of plants involved in DeWitt and Derby's (1955) high intensity burn was probably due to the increased productivity of completely top-killed plants. Shrub canopies in the low intensity burn probably suffered fractional mortality only. These relationships

suggest a need to reevaluate the effectiveness of prescribed burns conducted for game range improvement. Burns conducted too conservatively often are of insufficient intensity for optimal regrowth. Burning under these conditions wastefully removes ground fuels needed to carry fire while not meeting the objectives of stimulating shrub field productivity.

Acknowledgments

This work was funded by McIntire-Stennis project MS-22, College of Forestry, Wildlife and Range Sciences, University of Idaho, Idaho Forest, Wildlife and Range Experiment Station Paper No. 198. I thank M. Hironaka, L. Neuenschwander, and J. Peek for their review of this paper.

Literature Cited

Biswell, H. H., and A. M. Schultz. 1957. Surface runoff and erosion as related to prescribed burning. J. For. 55:372-375.

Bollen, W. B. 1974. Soil, nutrients, and waste, pp. B1-B34 *in* O. P. Cramer (ed.), Environmental Effects of Forest Residues Management in the Pacific Northwest: a State-of-Knowledge Compendium. USDA Forest Service Gen. Tech. Rep. PNW-24.

Cooperrider, A. Y., and D. F. Behrend. 1980. Simulation of forest dynamics and deer browse production. J. For. 78:85-88.

Daubenmire, R. F., and J. B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Washington Agric. Exp. Stn. Tech. Bull. 60.

DeWitt, J. B., and J. B. Derby, Jr. 1955. Changes in nutritive value of browse plants following fires. J. Wildl. Manage. 19:65-70.

Fowells, H. A., and R. E. Stephenson. 1934. Effect of burning on forest soils. Soil Sci. 38:175-181.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Washington Press, Seattle.

Isaac, L. A. 1963. Fire—a tool not a blanket rule in Douglas-fir ecology. Proc. Tall Timbers Fire Ecol. Conf. 2:1-18.

Mueggler, W. F. 1965. Ecology of seral shrub communities in the cedar-hemlock zone of northern Idaho. Ecol. Monogr. 35:165-185.

Neuenschwander, L. F., H. A. Wright, and S. C. Bunting. 1967. The effect of fire on a tobosagrass-mesquite community in the Rolling Plains of Texas. Southwestern Nat. 23:315-338.

U. S. Dept. of Commerce. 1976. Climatological data for Idaho. National Oceanic and Atmospheric Administration, Environmental Data Services, Asheville, North Carolina. 80:4.

———. 1977. Climatological data for Idaho. National Oceanic and Atmospheric Administration, Environmental Data Services, Asheville, North Carolina. 81:4.

———. 1978. Climatological data for Idaho. National Oceanic and Atmospheric Administration, Environmental Data Services, Asheville, North Carolina. 82:4.

Shearer, R. C. 1976. Early establishment of conifers following prescribed broadcast burning in western larch/Douglas-fir forests. Proc. Tall Timbers Fire Ecol. Conf. 14:481-500.

Short, H. L., R. M. Blair, and L. Burkart. 1972. Factors affecting nutritive values, pp. 311-318 *in* C. M. McKell, J. F. Blaisdell and J. R. Goodin (eds.), Wildland and Shrubs—Their Biology and Utilization. An International Symposium, Utah State Univ., Logan, Utah. U.S. Dept. Agr. Forest Service Gen. Tech. Rep. INT-1.

Tarrant, R. F. 1956. Effects of slash burning in some soils of the Douglas-fir region. Proc. Soil Sci. Soc. Amer. 20:408-411.

Received May 13, 1980
Accepted for publication October 20, 1980

W. H. Rickard

and

R. H. Sauer

Battelle Pacific Northwest Laboratories
Richland, Washington 99352

Self-Revegetation of Disturbed Ground in the Deserts of Nevada and Washington

Abstract

Plant cover established without purposeful soil preparation or seeding was measured on ground disturbed by plowing in Washington and by aboveground nuclear explosions in Nevada. After a time lapse of three decades in Washington and two decades in Nevada, fewer species were self-established on the disturbed ground than the nearby undisturbed ground. Alien annual plants were the dominants on the disturbed ground. Cheatgrass (*Bromus tectorum*) dominated abandoned fields in Washington, and filaree (*Erodium cicutarium*) dominated disturbed ground in Nevada. Perennial grasses and shrubs appeared to be more successful as invaders in Nevada than in Washington. This distinction is attributed to the superior competitive ability of cheatgrass in Washington.

Introduction

The orderly predictable process of self-revegetation of disturbed ground is termed ecological succession. Characteristically, the succession process is initiated by invasion of bared ground by annual plants having the capacity for copious seed production and efficient seed dispersal. Gradually, these annual plants are either suppressed or replaced by larger sized perennial plants until the next ground baring disturbance. In theory these perennials are the permanent members of the site, but they can be destroyed by sudden events such as fire, or diseases, or by man's activities such as mechanically disturbing the soil, or by the damage caused by domestic livestock. Although fire and disease have relatively little impact on the physical features of the rooting substrate, plowing or mechanical scraping not only destroys the plants but also disrupts the upper few decimeters of soil. Plowing itself is not generally considered to be a destructive process because it is conducted on the best soils which are promptly seeded to economically valuable crop plants. Because plowed ground in southeastern Washington is seldom allowed to become self-vegetated due to the economic value of cropping, there is little information on the rate or the terminal product of the self-revegetation process.

This study describes the species composition and canopy cover provided by plants on an abandoned cultivated field in the semi-arid shrub-steppe region of south-central Washington for comparison with land disturbed by nuclear explosions in the arid desert region of southern Nevada. Both sites have been essentially free from additional man-induced disturbances following the cessation of plowing and nuclear weapons testing which occurred 30 years ago in Washington and 20 years ago in Nevada.

Study Site

The Washington study site is located on the U.S. Department of Energy's Hanford Site in Benton County, Washington. Here, productive dryland wheat fields were aban-

doned in 1943 when the land was incorporated into the Hanford Site. The study field is located at an elevation of about 500 m above sea level and has a history of ecological study (Rickard *et al.*, 1973; Cline and Rickard, 1973; Hinds, 1973). The soil is at least one meter deep layered over basalt rock and is classified as Ritzville silt loam. The average annual precipitation over an eight year time span (1968-1975) averaged 25 cm (Hinds and Thorp, 1977). Precipitation falls mostly in fall and winter; snowfall is an annual event. The habitat-type is classified as *Artemisia tridentata/Agropyron spicatum* (Daubenmire, 1970). Since abandonment, the field has been occupied by a more or less closed sward of annual plants, especially cheatgrass (*Bromus tectorum*).

The Nevada site is located in Yucca Flat on the U.S. Department of Energy's Nevada Test Site in Nye County, Nevada. Many aboveground test explosions were conducted in Yucca Flat in the years 1950-1957; plant studies on the devegetated ground have been reported by Shields and Wells (1961), Rickard and Shields (1963), and Shields *et al.* (1963). The study site, Area T-2C, is located on a gentle slope along the western side of the valley. The elevation is approximately 1000 m above sea level. The soil substrate is of alluvial origin and is a heterogeneous mixture of rock and fine particles. The vegetation before nuclear testing was probably comprised of shrubs, mostly *Grayia spinosa* and *Lycium andersonii*, and a rich variety of small herbaceous species as described by Rickard and Beatley (1965). The study site was last used as a test area in the summer of 1957. In the early 1960s, some close-in mechanical blading was done at the site to scrape some persistent residual radioactive contaminants from the soil surface. The climate of Yucca Flat is arid: annual precipitation amounts to only 15 cm and on the average is equitably distributed throughout the year. Cattle grazed Yucca Flat in the years before it was incorporated as part of the Nevada Test Site, but grazing has been prohibited since the early 1950s.

Methods

Canopy cover was estimated using the method developed by Daubenmire (1959). In 1957, study lines consisting of 100 ft lines with 50 plots each (0.1 m^2) at two foot intervals were established in Yucca Flat by using marker stakes at 0.1-mile intervals eastward from ground zero of nuclear test "Shasta" to a distance of one mile (Rickard and Shields, 1963). It was hoped that these same study lines could be relocated after a time span of 20 years, but this operation was not possible. In the spring of 1978, 100 ft lines were established at 0.2, 0.3, 0.4, and 0.5 mi from ground zero and at 0.7, 0.8, 0.9, and 1.0 mi from ground zero. The first four lines were in the most heavily damaged zone (i.e., no vegetation remained after the explosion); the second four lines were in a zone with little visible damage. The ground slope is very gradual, with a drop in elevation of perhaps 5 m in 2000 m eastward into the central basin of Yucca Flat.

Four study lines were established on the Hartford Site Arid Lands Ecology Reserve. Two lines were located 20 m inside the boundaries of a 35-year-old abandoned cultivated field, and two lines were located in the relatively undisturbed vegetation *Artemisia/Agropyron* habitat type outside the old field boundaries. The field boundaries are still identifiable by a line of standing wooden fence posts. Plant names for Washington plant species follow Hitchcock and Cronquist (1973), and plant names for Nevada follow Beatley (1976).

Results and Discussion

Cheatgrass (*Bromus tectorum*) clearly dominated the canopy cover of longtime abandoned plowed ground in south-central Washington (Table 1). The adjacent relatively undisturbed vegetation in contrast was dominated by perennial grasses, especially bluebunch wheatgrass (*Agropyron spicatum*). Cheatgrass provided 24 percent of the total canopy cover in one undisturbed stand and only 1 percent in another. These two stands, however, probably have had different land use histories. Fire has been a factor in both stands, as evidenced by the presence of burned stumps of sagebrush. The year of the last fire was 1957 during a large burn that covered an estimated 50-60 mi^2. However, grazing use of the two sites was probably different. The stands are on opposing sides of a fence line that at one time separated wheat fields from rangeland. It is likely that the rangeland side of the fence was grazed much more heavily than the wheat side, resulting in an invasion by cheatgrass that has persisted for 30 years. More species were encountered on the two undisturbed (unplowed) sites than on the plowed field sites, but total canopy cover was greater on the plowed ground (Table 1).

Filaree (*Erodium cicutarium*) and red brome (*Bromus rubens*) dominated the canopy cover of severely disturbed ground at Yucca Flat (Table 2). The undisturbed ground supported twice as many plant species as the disturbed ground. There were also more plant species in Nevada than in Washington. Russian thistle (*Salsola* sp.) was more abundant in Nevada than in Washington.

As in Washington, fewer species occupy the disturbed than the undisturbed ground. Annuals are not an important component of vegetation of undisturbed ground in Washington, but they are an important part of the understory in Nevada (Rickard and Beatley, 1956). In Washington, undisturbed ground was dominated by perennial grasses, 67 percent canopy cover as compared to only 12 percent in Nevada (Table 3). Disturbed ground was dominated by annual grass, 88 percent canopy cover in Washington as compared to only 14 percent annual grass in Nevada. In both states, annual species of European origin were the most important invaders of disturbed ground. Cheatgrass and tumble mustard (*Sisymbrium altissimum*) were most important species in Washington; filaree, red brome, and Russian thistle were important in Nevada.

Although the process of secondary plant succession has often been described for moist, temperate forest communities, there is little information concerning the process in more arid regions (Drury and Nisbet, 1974). In recent years, surface mining for coal and uranium in the more arid grassland and desert regions of the western United States has created a need to revegetate severely disturbed ground promptly. The guidance for revegetation has been largely derived from agriculture and range management practices with little reference to the expected successional pattern. This procedure is not unexpected, as there are relatively few places in the West that are available for the long term observation of the self-revegetation process without concomitant man-induced land use interferences. The findings of this investigation are useful because lands that have been severely disturbed by man are studied. In our studies, there have not been any judgments made to predetermine what the end point use of revegetation should be—i.e., livestock grazing, wildlife habitat, or crops. This practice differs from conventional range management practices which aim to provide improved livestock forage, and it differs from agricultural practices which normally seek to increase yields of crop species. Our data indicate that self-establishment to dominance by perennial species can be a

TABLE 1. Canopy cover (%) covered by plants on ployed and unplowed grount in South Central Washington.

	Unplowed ground		Plowed ground	
	A	B	A	B
Annual Grasses				
Bromus tectorum[2]	0.7	24	95	97
Festuca spp.	0.4	1.6	0	0
Total annual grass	1.1	26	95	97
Average	14		96	
Annual Forbs				
Sisymbrium altissimum[2]	0	2.9	11	0.4
Plantago patagonica	0	2.6	0	0
Draba verna[2]	0.5	0.3	0	0
Descurainia pinnata	0	0.8	1.0	0.1
Holosteum umbellatum[2]	0	0	1.0	0.1
Amsinckia lycopsoides	0	0	0	0.1
Total annual forbs	0.5	6.6	13	0.7
Average	3.6		6.3	
Perennial Grasses				
Agropyron spicatum	33	31	0	0
Poa sandbergii	13	18	0.8	1.3
Stipa thurberiana	1.8	3.4	0	0
Stipa comata	1.6	0	0	0
Poa Cusickii	16	0	0	0
Total perennial grasses	64	52	0.8	1.3
Average	58		1.0	
Perennial Forbs				
Phlox longifolia	4.1	0.3	0	0
Astragalus sp.	0	3.4	0	0
Achillea millifolium	0.2	2.8	0	0
Lomatium macrocarpum	0	0.3	0	0
Lupinus sp.[3]	0	0	1.4	0
Microseris lanciniata	0.1	0	3.8	1.7
Antennaria dimorpha	0.1	0	0	0
Erigeron filifolius	0.7	0	0	0
Calochortus macrocarpus	0.6	0	0	0
Crepis atrabarba	1.1	0	0	0.9
Lupinus sp.	0.1	0	0	0
Tragopogon dubius[2]	0.2	1.0	2.8	1.1
Total perennial forbs	7.1	7.8	8.0	3.7
Average	7.4		5.8	
Shrubs				
Artemisia tridentata	7.2	0.1	0	0
Chrysothamnus viscidiflorus var. lanceolata	2.0	0	0	0
Total shrubs	9.2	0.1	0	0
Average	4.6		0	
Total Canopy Cover	82	92	116	103
Average	87		114	
Number of Taxa	19	15	7	9
Average	17		8	

[1]Burned, 1957; [2]Introduced species; [3]Seedlings only.

TABLE 2. Canopy cover % of plants on disturbed and undisturbed ground—Yucca Flat, Nevada.

	One-tenth mile intervals from ground zero T2c							
	Disturbed				Undisturbed			
Taxa	0.2	0.3	0.4	0.5	0.7	0.8	0.9	1.0
Annual Grasses								
Bromus rubens[1]	15	15	14	14	35	18	18	20
Total Annual Grasses	15	15	14	14	35	18	18	20
Average	14				23			
Perennial Grasses								
Stipa speciosa	3.6	0	0	0	5.0	2.8	0.4	2.9
Tridens pulchellus	4.0	2.8	2.8	8.6	0.3	0.3	0.4	0
Aristida longiseta	0.4	9.5	2.1	0	0	0	0	0
Oryzopsis hymenoides	0	0	0	5.9	0.5	8.1	0.7	1.1
Hilaria jamesii	0	0	0	0	1.4	0	2.6	9
Total Perennial Grasses	8.0	12	4.9	14	7.2	11	4.1	4.0
Average	9.7				6.6			
Annual Forbs								
Erodium cicutarium[1]	37	43	46	34	4.1	1.6	0.1	0.5
Salsola sp.[1,2]	2.6	1.7	2.3	2.3	6.0	1.7	2.0	1.0
Eriogonum nidularium	2.0	1.1	0.9	1.1	1.9	1.1	0.6	0.5
Cryptantha circumscissa	0.9	0.8	0.7	0.2	0.2	0.3	0.4	0.6
Sisymbrium altissimum[3]	0.1	0	0	0	0.5	0.4	0	0
Chaenactis steviodes	0.1	0.1	0	0	0	0	0.1	0.5
Mentzelia albicaulis	0.7	1.7	0.1	0.7	1.2	0.2	0.2	0.3
Camissonia kernensis	0	0.1	0	0.1	0	0	0.4	0.1
Euphorbia polycarpa (?)	0	0	0	0.7	0.5	0.6	0	0.1
Gilia sp.	0	0	0	0.1	0	0	0	0.4
Rafinesquia neomexicana	0	0	0	0	0.6	0	0.4	0
Oxytheca perfoliata	0	0	0	0	0.1	0	0.6	0
Syntrichopappus fremontii	0	0	0	0	0.8	0	0	0
Lupinus sp.	0	0	0	0	0.3	0	0.1	1.1
Lepidium lasiocarpum	0	0	0	0	0	0	0.6	0
Phacelia vallis-mortae	0	0	0	0	0	0	0.1	0.2
Compositae sp.	0	0	0	0	0	0	0.1	0.2
Eriophyllum pringlei	0	0	0	0	0	0	0	0.1
Oenothera sp.	0	0	0	0	0	0	0.1	0.2
Total Annual Forbs	43	48	50	39	16	6.9	6.7	7.6
Average	45				9.3			
Perennial Forbs								
Macheranthera sp.	0.3	0.1	0.5	0.1	0	0.1	0	0
Sphaeralcea ambigua	0	0	0.1	0.8	1.0	5.8	3.1	2.0
Dichelostemma puchellum	0	0	0	0	0.1	0	0	0.2
Astragalus lentiginosus	0	0	0	0	0	0	0	0.8
Total Perennial Forbs	0.3	0.1	0.6	0.9	1.1	5.9	3.1	3.0
Average	0.5				2.3			
Shrubs								
Hymenoclea salsola	0	0.3	1.9	0	2.9	5.4	4.5	0.6
Artemisia spinescens	0	0	0	0	0	0	0	0.3
Atriplex canescens	0	0	0	0	0.8	0.88	2.1	1.9
Grayia spinosa	0	0	0	0	0.7	0.1	0.6	0.7
Lycium andersonii	0	0	0	0	2.0	1.1	5.7	5.2
Ephedra nevadensis	0	0	0	0	0	0.3	1.1	5.5
Eurotia lanata	0	0	0	0	0	0	0.3	0
Haplopappus sp.	0	0	0	0	0	0	0	1.6

TABLE 2—(Continued)

Chrysothamnus viscidiflorus	0	0	0	0	0	0	0	1.6
Chrysothamnus nauseosus	0	0.9	0	0	0	0	0	0
Total Shrubs	0	1.2	1.9	0	6.4	7.7	15	16
Average			0.8				11	
Total Canopy Cover	67	77	71	69	66	50	47	50
Average			71				53	
Total number of taxa	12	12	11	13	22	19	26	27
Average			12				27	

[1]Introduced (alien) species, [2]Seedlings.

TABLE 3. Canopy cover % by plant categories on disturbed and undisturbed ground in Washington and Nevada and the percent of total canopy cover (%) provided by each plant category.

	Canopy Cover, %			
	Washington		Nevada	
Category	Undist.	Dist.	Undist.	Dist.
Annual grass	14 (16)	96 (88)	28 (47)	14 (20)
Annual forb	3 (>1)	6.3 (6)	10 (17)	45 (64)
Perennial grass	58 (67)	1 (<1)	7 (12)	10 (14)
Perennial forb	7.4 (11)	5.8 (5.3)	3 (5.0)	<1 (1)
Shrub	4.6 (5)	0 (0)	11 (19)	<1 (1)
Total	87 (100)	109 (100)	59 (100)	70 (100)

very slow process. It may not be possible to re-establish plant communities to pristine status in terms of species composition because of the ubiquitous presence of alien annuals that have successfully blended in with the native flora and seem to have altered the expected successional pattern of perennial grass and sagebrush dominance in Washington and desert shrub and annual forbs dominance in Nevada.

Acknowledgments

The authors are grateful for the support of Mr. E. Campbell, Department of Energy, Nevada Operations Office, in providing access to the Nevada Test Site and for the support of the Civil Effects Test Organization personnel located at Mercury, Nevada, for providing transportation and access to the herbarium.

The work was performed for the Department of Energy under Contract EY-76-C-06-1830.

Literature Cited

Beatley, J. C. 1976. Vascular Plants of the Nevada Test Site and Central-South Nevada: Ecological and Geographic Distribution. Technical Information Center, Oak Ridge, Tennessee.

———. 1966. Winter annual vegetation following a nuclear detonation in the northern Mojave Desert (Nevada Test Site). Radiation Botany 6:69-82.

Cline, J. F., and W. H. Rickard. 1973. Herbage yields in relation to soil water and assimilated nitrogen. J. Range Manage. 26:296-298.

Daubenmire, R. 1959. A canopy-cover method of vegetation analysis. Northw. Sci. 33:43-64.

———. 1970. Steppe Vegetation of Washington. Wash. Agric. Expt. Sta. Tech. Bull. 62.

———. 1975. Plant succession on abandoned fields and fire influences in a steppe area in southeastern Washington. Northw. Sci. 49:36-48.
Drury, W. H., and I. C. T. Nisbet. 1973. Succession. The Arnold Arbor. J. 54:331-368.
Hinds, 1973. Small lysimeters for measurement of water use and herbage yield. J. Range Manage. 26:304-306.
Hitchcock, C. L., and A. C. Cronquist. 1973. Flora of the Pacific Northwest—An Illustrated Manual. Univ. of Washington Press, Seattle.
Rickard, W. H., and J. C. Beatley. 1965. Canopy-cover of the desert shrub vegetation mosaic of the Nevada Test Site. Ecology 46:524-529.
———, and J. R. Murdock. 1963. Soil moisture and temperature survey of a desert vegetation mosaic. Ecology 44:821-824.
———, and L. M. Shields. 1963. An early stage in the plant recolonization of a nuclear target area. Radiation Botany 3:41-44.
———, J. F. Cline, and R. O. Gilbert. 1973. Behavior of winter annuals as influenced by microtopography and elevation. Northw. Sci. 47:47-49.
Shields, L. M., and P. V. Wells. 1962. Effects of nuclear testing in desert vegetation. Science 136: 38-40.
———, ———, and W. H. Rickard. 1963. Vegetation recovery in atomic target areas in Nevada. Ecology 44:697-705.
Thorp, J. M., and W. T. Hinds. 1977. Microclimates of The Arid Lands Ecology Reserve, 1968-1975. BNWL-SA-6231. Battelle, Pacific Northwest Laboratory, Richland, Washington.

Received March 18, 1980
Accepted for publication June 10, 1980

William B. Perry

and

Jack A. Stanford

Flathead Research Group
University of Montana Biological Station
Bigfork, Montana 59911

Algal Growth Stimulus by Phosphorus in Flathead Lake, Montana, Sediments

Abstract

Sediments from oligotrophic Flathead Lake stimulated more than double the growth of the algae *Selenastrum capricornutum* relative to control cultures in laboratory bioassays. Inorganic phosphorus, as well as other nutrients (e.g., nitrogen) in sediments were available as algal nutrients. These assays suggested that nutrients associated with sediments would likely stimulate algal growth in Flathead Lake. This growth apparently does not occur, because sediments derived from riverine sources have a short retention time in the photic zone of the lake. By inference we concluded that clay sediments entering the lake apparently play a functional role in sedimentation of phosphorus and other nutrients permanently to the lake bottom.

Introduction

Sediments may play a critical role in determining the trophic status of lakes, and a knowledge of the role of clay sediments is a concern in effective lake management (Serruya, 1971; Fillos and Swanson, 1975). Stanford and Potter (1976) suggested that the influx of clays during spring runoff influences the dynamics of the primary trophic level in Flathead Lake, Montana. The paucity of available phosphorus in this lake, 4-15 $\mu g\ l^{-1}$ (Stanford and Potter, 1976), probably makes this macronutrient an important one in directly influencing primary productivity.

Bottom sediments usually contain proportionately higher concentrations of nutrients than those found in the overlying water column due to gravitational losses of particulates (i.e., seston) and chemical precipitation. Consequently, sediments have long been recognized as a potential source of these nutrients to lake waters (e.g., Mortimer, 1941; Wetzel, 1975). However, little definitive information on the rate and extent of nutrient release from bottom sediments is available. The exchange of phosphorus between sediments and the overlying water appears to be dependent upon a number of chemical, physical, and biological parameters (cf. Lee, 1970; Wetzel, 1975). Laboratory studies (Golterman *et al.*, 1969; Porcella *et al.*, 1970) have shown that sediments may serve as the sole source of phosphorus to algae. Recent studies have attempted to quantify the different forms of sediment phosphorus and their potential as a macronutrient (cf. Wildung and Schmidt, 1973; Sagher *et al.*, 1975).

We performed laboratory bioassays to determine the biological availability of phosphorus in Flathead Lake sediments to a test alga, *Selenastrum capricornutum.* These experiments were a part of an ongoing study of the limnology of the Flathead Lake-River system to better define the functional role that clays may play in nutrient cycles within the lake.

Methods and Materials

Stock cultures of *Selanastrum capricornutum* were grown in synthetic assay medium mixed according to the *Selenastrum capricornutum* Prinz algal assay bottle test (U.S. EPA, 1978). In order to acclimate the alga, several successive cultures were grown in the AAP medium under the conditions of the assay. Since growth response relative to phosphate was to be examined, the alga was phosphorus-starved by growth under minus-phosphorus conditions. The medium used was AAP medium without the addition of the KH_2PO_4; KC1 was used to compensate for the potassium ion concentration. The alga was allowed to grow in AAP minus P medium (AAP-P) to maximum biomass in 50 ml. To ensure phosphorus limitation to growth, cells were then harvested by centrifugation, washed with distilled water, re-centrifuged, and transferred to fresh AAP minus P medium. The process was repeated until growth was less than 10 percent of controls over a 24-hr period. The P-starved *Selenastrum* were then used as inoculum for the assay.

A coring device was used to collect sediments in the deepest area of Flathead Lake (100 m) at a point near midlake and west of Yellow Bay. Sediment cores were kept frozen until used in bioassays. The top 5 mm of core was homogenized, dried at 105°C for 72 hr, crushed, and added to the assay media at a concentration of 1 gm l^{-1}.

The effect of sediments free of inorganic P upon algal growth was determined by using sediments treated with an extraction procedure employing high temperature ignition (Walker and Adams, 1958). This procedure was tested and evaluated against other commonly used methods (Jackson, 1955; Mehta *et al.* 1958) for the extraction of inorganic phosphorus from sediments and was judged to be the most suitable (Wildung and Schmidt, 1973). The method called for adding 100 ml of 1N N_2 SO_4 gm^{-1} of dried sediment followed by shaking for 16 hr. The sediment was then centrifuged, washed, centrifuged again, and then neutralized with NaOH. After drying and crushing, extracted and unextracted sediments were used in the assay. Of interest was the hypothesis that added sediment-phosphorus would significantly stimulate algal growth in comparison to controls in P-limited cultures. The bioassay was not, however, designed to differentiate between possible sources of inorganic phosphorus in the sediment, or their relative contributions to algal nutrition.

Six sets of three 50 ml replicates of the two experimental media (AAP and AAP-P) were inoculated with equal volumes of phosphorus-starved algae from the stock culture. Each culture set was then treated with extracted or unextracted sediments or untreated (controls) according to the experimental design shown in Table 1. An electronic particle counter (Coulter, Model ZBI) was used to determine cell numbers every 24 hr. Several cell counts were also made using standard microscopic procedures to ensure accuracy. Daily culture biomass (cell concentration) was calculated as an

TABLE 1. Experimental design and bioassay results; data are mean cell concentrations (cells $ml^{-1} \times 10^5$) $\pm$ 1 standard deviation (n = 3) at the conclusion of the bioassay (8 days).

Treatment	Medium	
	AAP-P	AAP
Unextracted sediment	50.4±12.8	64.0±2.0
Extracted sediment	7.2± 0.4	46.9±7.2
Controls (no sediment added)	5.0± 0.4	26.2±2.3

average of cell concentrations in each of the replicates within a given treatment. Significant difference between means was determined using a paired t-test ($= 0.05$).

Our bioassays examined only the biological availability of phosphorus, since not all forms of extractable inorganic phosphorus are available for algal nutrition. Some forms (i.e., apatite mineral, a form of occluded inorganic phosphorus) are not readily exchangeable (Li *et al.*, 1972) and were not considered to be a contributor to the dissolved phosphorus pool. These bioassays were designed to determine if inorganic phosphorus present in any form was available for algal growth under the test conditions.

Results and Discussion

The assays continued for 11 days; however, by day 9 all cultures had approached asymptotic growth. Cultures containing phosphorus (AAP medium) responded with growth that was significantly greater than observed in control cultures containing no phosphorus (AAP-P medium) (Table 1). Cultures in AAP-P medium containing extracted sediment were not significantly different from the AAP-P control cultures, which indicated that inorganic phosphorus had been removed by the extraction procedure (Table 1). Cell biomass in AAP control cultures was significantly less than cell biomass in the three other culture conditions (i.e., AAP plus extracted sediment, AAP plus sediment and AAP-P plus sediment) (Table 1). When sediments were added at the experimental concentration to AAP-P medium, final cell biomass was nearly twice that of the control cultures (Fig. 1). We concluded that sediment-phosphorus was available in sufficient quantity to stimulate a significant growth response.

We also concluded that other nutrients (e.g., nitrogen) were available in the sediments and that they apparently enhanced the stimulatory effect of phosphorus enrichment. The AAP cultures (containing 0.186 mg l^{-1} PO_4) treated with extracted sediments yielded greater biomass than AAP controls. Since significantly greater growth stimulus was not manifested in AAP-P cultures treated with extracted sediments in comparison to AAP-P controls, it was apparent that growth in AAP cultures was stimulated by nutrients other than phosphorus in sediments (Table 1).

Microscopic examination revealed that bacteria were present during the assays. Bacterial remineralization of particulate organic matter in the sediments may have been a factor affecting phosphorus availability to test algae. However, the within treatment standard deviations were not particularly great, indicating that bacterial remineralization and other bias effects were fairly uniform across the design.

Turbidity caused by sediment addition may have introduced a difference in light availability between control and treated cultures; this factor made direct comparisons of growth response to nutrient concentrations difficult. Small responses due to minor nutrient limitations may be difficult to detect quantitatively in such assays, unless differential illumination effects caused by sediment turbidity can be measured. However, available inorganic phosphorus concentrations were great enough in these experiments to offset potential light availability effects, and they resulted in clear growth stimuli.

The deep basin (mean depth = 50.2 m) of Flathead Lake restricts sediment resuspension, except in highly localized near-shore areas. Also, the water column is usually saturated with oxygen; anaerobic conditions, which may facilitate phosphorus release from the sediments (Mortimer, 1941; Lee ,1970), do not occur. These limnological conditions and the ability of the bottom sediments to supply phosphorus in the bio-

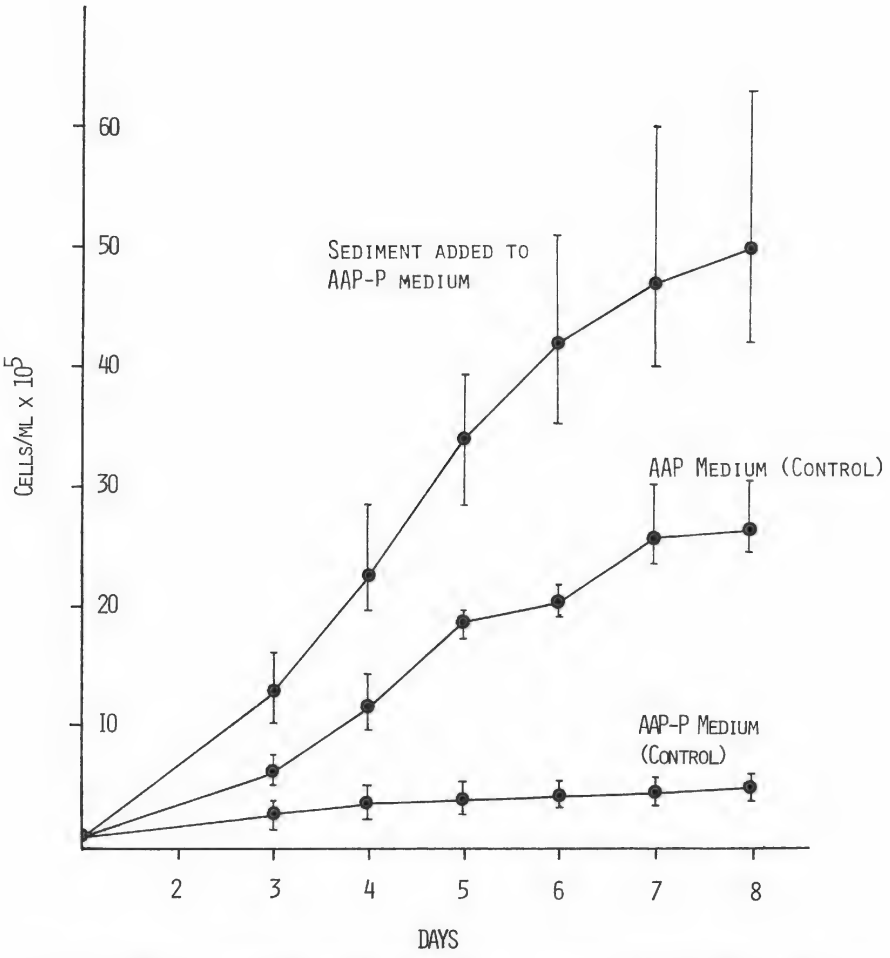


Figure 1. Growth of *Selenastrum* (means and ranges) in P-limited (AAP-P) and normal (AAP) control cultures in comparison to P-limited cultures treated with unextracted sediments from Flathead Lake.

assay implied that Flathead Lake sediments may expedite the permanent loss of this macronutrient from nutrient cycles in the lake. The low concentrations of phosphorus in the water and the higher concentrations of phosphorus in the profundal sediments add support to the hypothesis (Stanford and Potter, 1976) that sedimenting clays introduced during spring runoff may play a role in limiting primary productivity.

Acknowledgments

The bioassays were completed in the Limnology Laboratory at North Texas State University, Denton, Texas. Financial and material support was provided by the NTSU Faculty Research Committee and University of Montana Biological Station. We thank

Delano Hanzel, Montana Department of Fish, Game and Parks, for help in obtaining sediment cores.

Literature Cited

Fillos, J., and W. R. Swanson. 1975. The release rate of nutrients from river and lake sediments. J. Wat. Poll. Contr. Fed. 47: 1032-1042.

Golterman, H. L., C. C. Badels, and J. Jakobs-Mogelin. 1969. Availability of mud phosphates for the growth of algae. Verh. Internat. Verein. Limnol. 17: 467-479.

Jackson, M. L. 1958. Soil Chemical Analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.

Lee, G. F. 1970. Factors affecting the transfer of materials between water and sediments. U. Wis. Wat. Res. Centr. Lit. Rev. No. 1.

Li, W. C., D. E. Armstrong, J. D. H. Williams, R. F. Harris, and J. K. Syers. 1972. Rate and extent of inorganic phosphorus exchange in lake sediments. Soil Sci. Soc. Amer. Proc. 36: 279-285.

Mehta, N. C., J. O. Legg, C. A. I. Goring, and C. A. Black. 1954. Determination of organic phosphorus in solids: I. Extraction method. Soil Sci. Soc. Amer. Proc. 18: 443-449.

Mortimer, C. H. 1941. The exchange of dissolved substances between mud and water in lakes. J. Ecol. 29: 280-329.

Porcella, D. B., J. S. Kumagai, and E. J. Middlebrooks. 1970. Biological effects on sediment-water nutrient interchange. J. Sanitary Eng. Div., Prov. Amer. Soc. Civil Eng. SA4: 911-926.

Sagher, A., R. F. Harris, and D. E. Armstrong. 1975. Biological Availability of Sediment Phosphorus to Microorganisms.. Water Resources Technical Report: OWRT A-040-WIS. Univ. of Wisconsin, Madison.

Serruya, C. 1971. Lake Kinneret: the nutrient chemistry of the sediments. Limnol. Oceanogr. 16: 510-521.

Stanford, J. A., and D. S. Potter. 1976. The Flathead Lake River ecosystem: a perspective, pp. 241-250 *in* Andrews, R. D. III, *et al.* (eds.) Terrestrial and Aquatic Ecological Studies at the Northwest Symposium Proceedings, March 26-27, 1976. Eastern Washington State College Press, Cheney.

U.S. Environmental Protection Agency. 1978. The *Selenastrum capricornutum* Prinz Algal Assay Bottle Test. Corvallis Environmental Research Laboratory, Corvallis, Oregon.

Walker, T. W., and A. F. R. Adams. 1958. Studies on soil organic matter. Soil Sci. 85: 307-318.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co., Philadelphia, Pa.

Wildung, R. E., and R. L. Schmidt. 1973. Phosphorus Release from Lake Sediments. Proj. 16010 DUA. National Eutrophication Research Program, Environmental Protection Agency, National Environmental Research Center. EPA Res. Series: EPA-R3-74-024.

Received March 20, 1980
Accepted for publication July 7, 1980

D. Lynne Kemper

14611-89th Ave.
Edmonton, Alberta T5R 4P4

and

J. Mary Taylor

Department of Zoology
The University of British Columbia
Vancouver, B.C. V6T 1W5

Photoperiod Experiments on the American Robin (Turdus migratorius L.)

Abstract

The American Robin of southwestern British Columbia was tested in captivity under four light regimes: LD 8:16, 12:12, 16:8, all under artifical light, and natural daylight increment from LD 12:12 to 16:8. Robins under the latter two regimes gained in gonadal weight and in follicular and seminiferous growth, and the males developed spermatocytes and, under natural light, spermatids. Perch activity was monitored in the groups on LD 8:16 and on natural photoperiod. The group on short controlled daylength was inactive on the perch at night, whereas that on natural photoperiod was very active in the first half of the dark period, activity that is possibly related to nocturnal movement in the wild.

Introduction

Northward migration and the caroling dawn chorus of the American Robin (*Turdus migratorius* L.) herald the arrival of spring in most portions of North America. Timing of this predictable annual event and the phenology of reproductive stages have long been associated in this species with geographical and climatological features. Recent studies that examine this relationship are those of James and Shugart (1974) and of Knupp, Owen, and Dimond (1977).

The abundance of the American Robin and its widespread distribution and habitat selection make this species an ideal candidate for tests involving manipulation of environmental parameters which may affect the timing of its migration and reproduction. For about 60 species of north Temperate birds, increasing daylength has proven to be a powerful influence on gonadal recrudescence and migratory behavior (Immelmann, 1971). Photostimulation has induced males into spermatogenesis and females into early stages of ovarian development (Immelmann, 1971). Our study tested both for gonadal response and for evidence of possible migratory restlessness. To our knowledge, this is the first study of this species that examines and experimentally alters a feature of the environment—in this case, photoperiod—under test situations.

Methods and Materials

The tests were performed on the campus of The University of British Columbia, Vancouver, in conjunction with a field study of the breeding biology of robins in the same area (Kemper and Taylor, 1981). Two sets of controlled photoperiod experi-

ments were designed to demonstrate the effect of altered photoperiod on gonadal development. One also tested for migratory restlessness. Caged birds were housed under natural daylight for one week prior to testing.

In the first experiment, 21 robins were maintained on three different light regimes. One group (4 males, 2 females) was given a light:dark (LD) cycle of 8:16 hours, respectively. Another group (7 males, 1 female) was maintained on LD 12:12, and the third group (6 males, 1 female) received LD 16:8. Experimental conditions began 1 February and the birds were sacrificed on 19 April.

Groups of three to five birds were housed in wire cages 120 x 60 x 60 cm. Each cage was provided with one perch, one food dish, and one water dish. Commercial chick starter, ground beef, and water were freely available. The cages were enclosed by a 6 mil black vinyl plastic which effectively blocked all natural light. Illumination was provided by a single 20-watt cool white fluorescent light for each cage. This light emits an average of 1150 lumens. The cages were outside and exposed to ambient outdoor temperatures.

In the second experiment, conducted outdoors from 6 March to 5 May, two photoperiods were maintained: one was LD 8:16 (2 males, 1 female), and the other was the natural daylight photoperiod of the area for the duration of the experiment (3 males). The six robins were housed individually in cages 35 x 40 x 40 cm containing a food dish, a water dish, and a single perch. The perch was connected to a microswitch that tripped when the bird hopped on or off. The switch connected to an Esterline-Angus 20-channel event recorder. The three robins on LD 8:16 were illuminated and protected against interfering light by the same means as those of the previous experiment. These three were tested against the three on natural photoperiod, in which daylight (including civil twilight) increased from 12 to 16 hours.

The birds were sacrificed and the gonads weighed and fixed in Bouin's solution for histological preparation at the end of the experiments. One testis from each male was embedded in paraffin, sectioned at 7μ, and stained with Delafield's hematoxylin and eosin. The slides were examined for tubule diameter and stage of sperm development. The number and size of developing follicles were recorded for each ovary.

Results

First Experiment

Changes in testicular development of males on different photoperiods are summarized (Table 1). Neither the LD 8:16 nor the LD 12:12 groups showed any histological

TABLE 1. Testis weight and seminiferous tubule diameter at the conclusions of the photoperiod experiments.

	N	Testis weight (mg) of a pair (mean, standard error, and range)	Seminiferous tubule diameter (μ) mean, standard error, and range)	Sperm
First experiment				
LD 8:16	4	20.0±8.4 (8.2-39.2)	39.4±0.9 (37.8-41.2)	—
LD 12:12	7	26.6±8.4 (12.3-59.4)	45.0±9.1 (30.9-72.8	—
LD 16:8	6	390.7±77.9 (174.7-617.5)	110.3±9.0 (82.9-143.1)	—
Second experiment				
LD 8:16	2	34.0, 61.9	7.6, 21.9	—
LD Natural Daylength (12:12 - 16:8)	3	623.2±106.6 (441.1-810.2)	124.7±1.73 (121.1-126.7)	—

evidence of testicular recrudescence, whereas the group on the LD 16:8 developed spermatocytes but no sperm. The natural daylength at the termination of the experiment was 15¾ hours, by which time wild male robins are spermatogenic (Kemper and Taylor, 1981).

The two females on LD 8:16 had ovarian weights of 26.8 mg and 40.9 mg and showed no follicular development (follicular diameter averaged 0.5 mm). The ovary of the single female on LD 12:12 weighed 56.8 mg and similarly showed no follicular development, but that on LD 16:8 weighed 183.1 mg and had nine follicles, two of which were 2 to 3 mm in diameter. In early February, wild robins show no sign of follicular activity, but 19 April, the day the tests were terminated, is at the onset of the height of breeding activity in the wild (Kemper and Taylor, 1981).

Second Experiment

Males on LD 8:16 showed no development of secondary spermatocytes or presence of spermatids at the end of this experiment in early May. Testis weight and seminiferous tubule diameters are given in Table 1. The ovary of the female under this treatment weighed 28.3 mg, and follicles averaged 0.5 mm in diameter. Males on naturally increasing daylength had the largest testes of any captive group. Developing spermatocytes and spermatids were plentiful, but mature sperm were absent. Testes weights of these captives are comparable to those of wild robins sampled on 5 May, the same day; however, wild birds with seminiferous tubule diameters that exceed 120μ show full spermatogenic activity (Kemper and Taylor, 1981).

Perch activity of both photoperiod groups is presented in Figure 1. In most instances, the activity index of the group on natural photoperiod was considerably greater in the first half of darkness than in the remaining dark period, and in daylight hours was generally well below that of the group on shortened photoperiod.

Discussion

Annual periodicity in daylight has been demonstrated to be a control system in the reproductive cycle of about 60 north Temperate species of birds. Included are *Junco oreganus shufeldti* (Wolfson, 1942) and *Zonotrichia leucophrys pugetensis* (Farner, 1975), species that are sympatric breeders with the American Robin in southwestern British Columbia. Our two sets of experiments, designed to test stimulatory influences of increasing daylength on gonadal development in the American Robin, showed a positive correlation. Although males showed more gonadal response than females, in neither sex did the test birds attain a reproductive state comparable to that of wild breeding robins.

A factor in our experimental design that may have retarded or inhibited full gonadal recrudescence is quality of light. The light source used emits light mainly in the yellow portion of the visible spectrum, between 545 and 575 Å, with another less powerful emission at the blue portion that peaks at 440 Å. Male Starlings (*Sturnus vulgaris*) respond gonadally to full spermatogenic activity only between 580 and 680 Å. In the same spectral region that was used in our experiments, Starlings either progressed no farther than the spermatocyte stage or sperm production was very reduced (Burger, 1943).

It is unlikely that intensity of light was a deterrent to sexual recrudescence in our

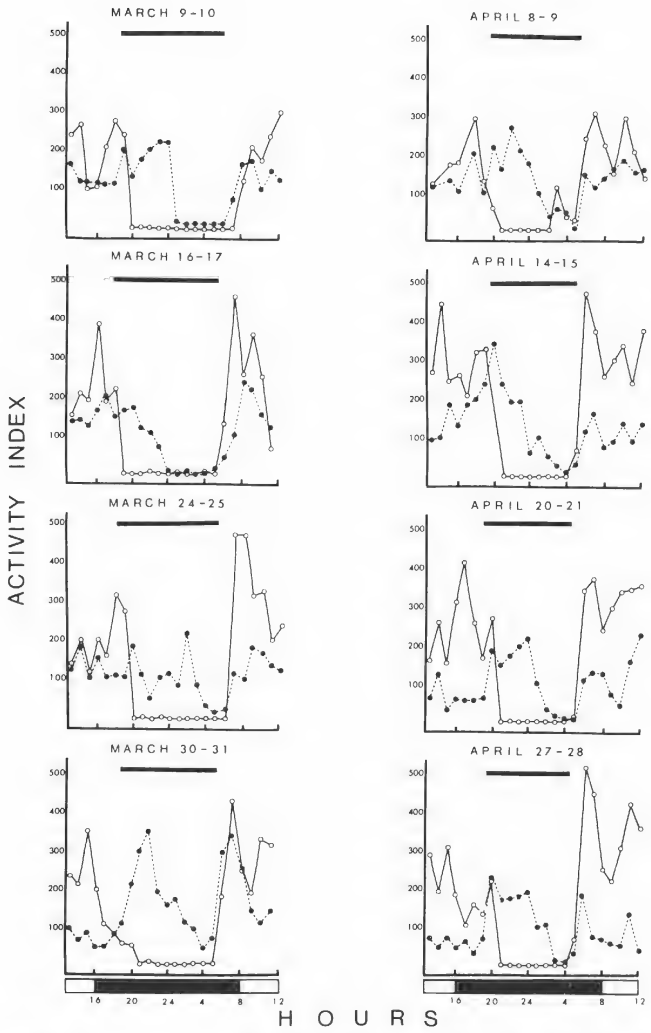


Figure 1. The perch activity for the LD 8:16 group and the group on natural daylength increment is represented by open circles and solid lines and by solid circles and dotted lines, respectively. The plots are averaged by group. Each graph represents one 24-hour period each week for 8 weeks, from 9 March to 28 April. The period from 16:00 hours to 8:00 hours the next morning is the dark phase of the birds on LD 8:16; it is indicated as the dark area of the hours bar at the bottom of the figure. The dark portion of the changing natural daylength, to which only the second group was exposed, is indicated by a fine bar at the top of each graph.

experiments. In both sets of experiments that used fluorescent lighting, the robins received 60-120 foot-candles of light at the bottom of the cage farthest from the light source and greater amounts elsewhere. This range of intensity is much higher than the minimum required in early spring to elicit gonadal response in, for example, the English Sparrow, *Passer domesticus* (Menaker, 1971).

The second experiment also examined whether artificially shortened photoperiod would inhibit nocturnal restlessness during a migratory period, as has been shown for many other North American species (Rowan, 1926; Wolfson, 1942, 1959; Farner, 1955; Farner *et al.*, 1960). Virtually no night activity was expressed by robins on LD 8:16 photoperiods, whereas those on longer days underwent such activity at levels comparable to their diurnal activity, from the first test (9-10 March) five days after the start of experimental conditions to the conclusion of the test period, a span of almost two months (Fig. 1).

Few attempts have been made to discover whether the American Robin is a nocturnal or diurnal migrant, or both (Graber, Graber, and Kirk, 1971). Our results suggest that the strong nocturnal component of the cage activity under conditions of increasing daylength may be expressed as nocturnal movement of this species in the wild. This interpretation is tentative, however, because some question exists as to whether nocturnal restlessness in birds can really be equated with a physiological state of migratory behavior (see Berthold, 1975, for discussion).

Acknowledgments

This project was supported by grant A-3462 from the National Research Council of Canada awarded to J. M. Taylor. Mrs. Sarah C. Smith prepared the figure for this paper and assisted in library searches. Dr. J. W. Kamp and Dr. C. M. Kemper provided a critical reading of the manuscript.

Literature Cited

Berthold, J. 1975. Migration: control and metabolic physiology, pp. 77-128 *in* Farner, D. S., and J. S. King (eds.). Avian Biology. Vol. 5, Academic Press, New York.

Burger, J. W. 1943. Some effects of colored illumination on the sexual activation of the male Starling. J. Exp. Zool. 94:161-168.

Farner, D. S. 1955. The annual stimulus for migration: experimental and physiological aspects, pp. 198-237 *in* Wolfson, A. (ed.). Recent Studies in Avian Biology. Univ. Illinois Press, Urbana.

———. 1975. Photoperiodic controls and reproductive cycles in *Zonotrichia*, pp. 369-382 *in* Frith, H. J., and J. H. Calaby (eds.). Proceedings of the 16th International Ornithological Congress. Australian Acad. Sci., Canberra.

———, A. Oksche, F. I. Kamemota, J. R. King, and H. E. Cheyney. 1960. A comparison of the effect of long daily photoperiod on the pattern of energy storage in migratory and non-migratory finches. Comp. Biochem. Physiol. 2:125-142.

Graber, R. R., J. W. Graber, and E. L. Kirk. 1971. Illinois Birds. Turdidae. Illinois Nat. Hist. Surv. Biol. Notes 75.

Immelmann, K. 1971. Ecological aspects of periodic reproduction, pp. 341-389 *in* Farner, D. S., and J. R. King (eds.). Avian Biology. Vol. 1, Academic Press, New York.

James, F. C., and H. H. Shugart, Jr. 1974. The phenology of the nesting season of the American Robin (*Turdus migratorius*) in the United States. Condor 76:159-168.

Kemper, D. L., and J. M. Taylor. 1981. Seasonal Reproductive Changes in the American Robin (*Turdus migratorius* L.) of the Pacific Northwest. Canadian J. Zool. 59:212-217.

Knupp, D. M., R. B. Owen, Jr., and J. B. Dimond. 1977. Reproductive biology of American Robins in Northern Maine. Auk 94:80-85.

Menaker, M. 1971. Rhythms, reproduction and photoreception. Biol. Reprod. 4:295-308.

Rowan, W. 1926. On photoperiodism, reproductive periodicity, and the annual migrations of birds and certain fishes. Proc. Boston Soc. Nat. Hist. 38:147-189.

Wolfson, A. 1942. Regulation of spring migration in juncos. Condor 44:237-263.

———. 1959. The role of light and darkness in the regulation of spring migration and reproduction in birds, pp. 679-716 *in* Withrow, R. B. (ed.). Photoperiodism. AAAS, Washington, D.C.

Received May 31, 1980
Accepted for publication August 1, 1980

Thomas H. Lewis
1505 Avenue D
Billings, Montana 59103

Contributions to Paleontology by an Early Montana Physician

Abstract

Dr. J. C. F. Siegfriedt was a physician in Montana from 1904 to 1940, a politician (mayor and state senator), an indefatigable booster of his community, and an enthusiastic naturalist with substantial scientific accomplishments. He made the first discovery and participated in the subsequent study of a unique faunal assemblage (Bearcreek) from the early Paleocene. The assemblage contained primates and insectivores, one of which bears his name (*Entomolestes seigfriedti*). He was an early supporter of the Yellowstone Bighorn Research Association, which has been a distinguished teaching institution.

John Charles Fredrich Siegfriedt was born in Davenport, Iowa, on 25 June 1879. He graduated from the College of Physicians and Surgeons, University of Illinois, in 1902, and came to Bearcreek, Montana, in 1904. He practiced there and in Red Lodge. He served as State Senator from 1920-1924 and was mayor of his town when he died in 1940. Throughout his life he was an enthusiastic student of geology and paleontology. His duties as a mine physician gave him opportunity to become a serious investigator, and his work led to significant discoveries. He initiated the formal scientific delineation of the coal measures of Carbon County and the description of a unique Paleocene faunal assemblage, one species of which bears his name. He suggested and helped to establish the Yellowstone Bighorn Research Association, an institution of research and teaching which has grown to be a permanent part of Montana's academic resources. It is today a thriving teaching facility of solid reputation, with faculty drawn from several American universities and summer classes of about sixty students from the United States and abroad.

Geologic interest in Bearcreek began with the examination of sedimentary strata formed in the early Cretaceous. In that Period a vast geosyncline extended from the Gulf of Mexico to the arctic. Into the lakes and seas which intermittently filled this trough were deposited sediments which eventually measured tens of thousands of feet in thickness and contained marine, lacustrine, and lagoonal fossils. Most of the Montana coal was deposited during this era, and at the end of it, these enormous layers were slowly upthrust, folded, faulted, arched, and overthrust. Thus, a prominent mountain system along the old north-south axis was built. During the thirty million years of Paleocene, and Eocene which followed, erosion smoothed this contorted mass; by the Miocene, twenty-five million years ago, these Ancient Rockies were worn down into a continental plain, the mountain roots and cores buried in their own debris, and the rivers were taking new directions along new planes. In the nine million years of the Pliocene, and in the Pleistocene, uplifting and folding created the present Rocky Mountain chain. South of Red Lodge, in related vulcanism, the Absaroka Mountains were being built. The Mesozoic faunas (predominantly reptilian) were succeeded in the Paleocene by increasing numbers of primitive birds and mammals, and by the in-

creasing dominance of flowering plants, many of these similar to today's genera. The Paleocene is represented in southern Montana and northern Wyoming by the enormous thickness of the Fort Union formation, and in it, by the distinctive Bearcreek mammals.

On 5 November 1926, Dr. J. C. F. Siegfriedt examined a piece of carbonaceous shale on the top of a loaded coal car at the pit-head and saw exposed a blackish tooth which looked very much like a recently extracted molar. Siegfriedt was in equal parts a scientist and a civic booster. He spoke in a serious way to his paleontological colleagues and with fervid enthusiasm to the press. This two-pronged approach to matters was repeatedly expressed in his life and nowhere more vividly than in this instance. The tooth specimen was photographed in Red Lodge by William Lewis and appeared in the Carbon County *News* as "evidence of early man, millions of years old." The tooth, now lost, was in due course accurately identified as belonging to a condylarth (possibly *Phenacodus*), a group ancestral to the hoofed mammals of today: It was the first of an extensive collection of teeth and bone fragments found in a dark-colored, bituminous clay-like layer just above Seam 3 in the Eagle Mine, Bearcreek.

Dr. Siegfriedt wrote to Henry Fairfield Osborn in September 1927 about this material, and later sent his collections to the American Museum of Natural History. Dr. Barnum Brown visited the site in September 1927; with Siegfriedt, Brown made further collections of fragments and matrix. The fossiliferous stratum was described as about 1500 feet above the base of the Fort Union formation, and from it scholars have since drawn rich materials. George Gaylord Simpson (1928) published on this new Paleocene mammalian fauna, describing a new mammalian family, four new genera, and five new species, including *Leipsanolestes siegfriedti*, a primitive insectivore. The new genus and species was later revised to *Leptocodon siegfriedti* and is now known as *Entomolestes siegfriedti.*

Revisions of and additions to this unique assemblage continued (Simpson, 1929 a, b) with thirty species of vertebrates ultimately being described, including a new rodent (Jepson, 1937), arboreal insectivores, small lemur-like primates, precanids and other predaceous carnivores, herbivores, and others (Van Valen and Sloan, 1966; Delson, 1971). All of the Bearcreek fauna dates to the early Paleocene. David C. Parris, Curator at the New Jersey State Museum, is presently engaged in a comprehensive study of all these forms and describes them (1980, pers. comm.) as "inhabitants of a terminal swamp, that is, the final stages in the sediment-filling of a sizeable lake in the basin . . . it is one of the earliest localities that contain fossil rodents (a few nearby rodent localities are about the same age)." In addition to the mammals there are crocodiles, turtles, a salamander, and a *champsosaurus* (a small, long-snouted amphibious dinosaur), all characteristic of a coal-forming swamp or bog near forests. In this fauna, 30 species of vertebrates are now known.

In the summer of 1930, members of the Scott Fund Expeditions, Princeton University, found dinosaur egg shell fragments on Dry Creek, the first to be reported from North America. The locality is on a ridge south of the old Ohio Oil Company camp, now a small community about eight and one-half miles northeast of Red Lodge. The press had given intemperate coverage to the Mongolian discoveries of dinosaur eggs by Roy Chapman Andrews a short time before, and the enthusiasm of newspaper reporters over the egg shell fossils of the American great reptiles must have annoyed the scientists. In the following January, Dr. Glenn L. Jepsen (1931) published a

factual description of the material, prefaced by extended acerbic remarks about exaggerations, distortions, fantasies, and "mystic reports" which had already appeared in the lay press. Dr. Jepsen and E. J. Moles, Jr. (of the Princeton staff) had spent part of that summer of 1930 near Red Lodge at the invitation of Dr. Siegfriedt on a practical, commercially important effort to define, as a guide to gas and coal development, the lower limits of the Fort Union formation. The stratigraphic elements and boundaries had been studied in nearby Wyoming where a Lower Fort Union fauna had been found just above the dinosaur-bearing Lance (Cretaceous) shales. As a logical extension of these studies toward the coal measures and gas-oil exploration of Red Lodge and Bearcreek, the sandstone and shale exposures near the Ohio Oil Company camp on Dry Creek promised further information. Dinosaur fossils were subsequently found associated with a mammal tooth (mammals being rare in the Lance). Further investigation disclosed small bits of dark brown egg shell, slightly curved, and perforated with numerous fine pores. They were comparable to the Mongolian dinosaur egg shells (which were more nearly intact) in micro-structure and gross appearance, and different from turtle, crocodilian, or bird embryo-containers. Intact eggs were not found, and have not yet been found, but stories still current describe Siegfriedt's delight over elaborate practical jokes he arranged for the misdirection and discomfiture of rival investigators and reporters. In July 1977, John Horner discovered a fragment of a dinosaur egg (Princeton University Natural History Museum No. PU 22236) in the Two Medicine Formation, Powder County, Montana, a discovery which awaits further elucidation.

The liveliest description of Siegfriedt by a contemporary was given by Dr. Jepsen in a letter to Dr. Erling Dorf read at a Princeton University Conference on the Central and Northern Rocky Mountains in August 1974, honoring Dr. Dorf. The letter, published in a memorial to Dr. Jepsen by the Department of Geological and Geophysical Science, Princeton University, 4 March 1975, is quoted below:

> Remember the "Paleontologist at Large," the self-appointed President of apocryphal Beartooth University, Dr. J. C. F. Siegfriedt? He regarded the study of any geology except fossils and oil fields as a complete waste of time. To him, isostasy, a big deal in those days, was a perversion of effort, and he was very vocal about it. Planks in his platform when he ran for Mayor of Red Lodge in 1937 were "bring in twenty more slot machines" and "start some new houses of pleasure." He won.
>
> His efforts were principally responsible for the construction of the highway through the Beartooths where, in accord with his wish, his ashes were scattered after his sudden death in his office, hat and satchel in hand, in 1940.
>
> His ecstasy was explosive and uncontrollable when Ted Moles (swimmer and student) and I found fragments of the first dinosaur eggs to be recovered in the Western Hemisphere, at Dry Creek, a few miles east of Red Lodge. He published a picture of a small hill, several miles away, as the "original site" and, through binoculars, watched with complete pleasure as the members of the group he had thus baited spent several torrid days with heavy machinery digging for more. "That fixed the sons of bitches" he gloated as the story spread.
>
> His discovery of the first fossil vertebrate, a tooth, from the Fort Union coal mines at Bear Creek was the event that triggered his delight with paleontology. He claimed that the tooth was human and that Bear Creek was the Garden of Eden. Most of the hundreds of recovered fossil bones came from a thin bed of "gob" (shaly coal or coaly shale) above the main coal seam, and this two-inch layer of late Paleocene history revealed a unique ecologic setting with an assemblage of vertebrates (a "faunule") unknown anywhere else in the world. It has become an internationally famous challenge to interpretation, a treasury of geobiologic unorthodoxy. Some kinds of Early Tertiary mammals that should be there are not, although they have been found by Princeton students by the thousands in the rocks of similar age around nearby Polecat Bench.

Princeton University studies in the Bighorn Basin were fundamental in delineating the stratigraphy and relationship between the reptilian (dinosaur) fossils of the Cretaceous and the abundant (about one hundred genera in North America) mammals of

the Paleocene. At the other nearby sites, as at Bearcreek, teeth and jaws of primitive primates, which lived about sixty million years ago, were abundant. The studies at Rock Bench Quarry, Polecat Bench, Dry Creek, and elsewhere helped toward the establishment of the Yellowstone Bighorn Research Association, first in tents at Siegfriedt's "Piney Dell" above Red Lodge in 1930, later with permanent buildings. Regular summer geology courses for university credit were offered in field techniques, mapping, and structural geology. Although the work of many went into the establishment of the Research Association, Dr. Siegfriedt characteristically supplied his full measure of enthusiasm. The group, according to the Red Lodge *Pickett-Journal* of 12 June 1930, was sponsored by Princeton University, the University of Montana, and the Montana Bureau of Mines. Dr. William T. Thom, Jr. (Princeton) and Dr. J. P. Rowe (University of Montana), the chief administrators, were assisted by Dr. R. M. Field and Dr. Erling Dorf (Princeton). Guest scientists were expected for the opening sessions, from Cambridge University, University of Freiburg, Institute of Aachen, and Charles University of Prague. Local supporters were J. F. Brophy, O. J. Rice, William Freakes, and Dr. J. C. F. Siegfriedt; assistance by the Northern Pacific Railroad Company and Senator Thomas J. Walsh was acknowledged. A *Pickett-Journal* article on 26 June 1930 gave a somewhat different table of organization and announced an International Congress of Geology and Paleontology for 1932. The Carbon County *News* had articles on Siegfriedt's camp in 9 April, 11 June, and 18 June 1931, and on 22 June 1932.

A history of the organizational and scientific development of the Yellowstone Bighorn Research Association has been written by Michael Kennedy (1979). Unfortunately, Siegfriedt himself never published.

Literature Cited

Delson, Eric. 1971. Fossil Mammals of the Early Wasatchian Powder River Local Fauna, Eocene of Northeast Wyoming, pp. 307-364 in Bulletin of the American Museum of Natural History, Vol. 146.

Jepsen, Glenn Lowell. 1973. A memorial printed by Princeton University Faculty, Department of Geological and Geophysical Sciences, 4 March 1973.

———. 1931. Dinosaur Egg Shell Fragments from Montana. Science 73:12-13.

———. 1937. A Paleocene Rodent, *Paramys atavas*. Proc. of the Am. Philos. Soc. 78:291-301.

Kennedy, Michael. 1979. Yellowstone-Bighorn Research Association Camp, pp. 283-284 *in* Shirley Zupen and Harry J. Owens, Red Lodge: Saga of a Western Area. Billings Frontier Press, Montana.

Scott, W. B. 1937. A History of Land Mammals in the Western Hemisphere. Rev. Ed. 1937. Macmillan Co., New York.

Simpson, George Gaylord. 1928. A New Mammalian Fauna from the Fort Union of Southern Montana. American Museum Novitates. No. 297.

———. 1929. A Collection of Paleocene Mammals from Bear Creek, Montana. Annals Carnegie Mus. 19:115-122.

———. 1929. Third Contribution to the Fort Union Fauna at Bear Creek, Montana. American Museum Novitates. No. 345.

Van Valen, Leigh. 1967. New Paleocene Insectivores and Insectivore Classification. Bull. Am. Mus. Nat. Hist. 132:217-284.

———, and Robert E. Sloan. 1966. The Extinction of the Multituberculates. Systematic Zoology 15:261-278.

Received February 3, 1981
Accepted for publication March 11, 1981

W. H. Rickard

W. C. Hanson

and

R. E. Fitzner

Battelle Pacific Northwest Laboratories
Richland, Washington 99352

The Non-Fisheries Biological Resources of the Hanford Reach of the Columbia River[1]

Abstract

The Hanford Reach is the only undammed segment of the Columbia River in the United States upstream from Bonneville Dam. The non-agricultural and non-recreational land-use policies imposed by the Department of Energy have permitted the Hanford Site to function as a refugium for wildlife for 35 years. The protection offered by the Hanford Site has been especially important for the Bald Eagle (*Haliaeetus leurocephalus*), mule deer (*Odocoileus hemionus*), coyote (*Canis latrans*), and resident Great Basin Canada Goose (*Branta canadensis moffitti*). Island habitats are especially important for nesting geese and for mule deer fawning. Coyotes are important predators upon nesting geese and mule deer fawns. Salmon carcasses are an important winter food for Bald Eagles.

Riparian plant communities along the Columbia River have been changing in response to changing water level fluctuations largely regulated by power generation schedules at upstream hydroelectric dams. There are no studies presently established to record the response of Columbia River shoreline plant communities to these kinds of fluctuating water levels.

The existing information is summarized on birds and mammals closely allied with the Hanford Reach of the Columbia River. High trophic level wild animals are discussed as indicators of chemical contamination of food chains.

Introduction

The Hanford Reach of the Columbia River extends upstream from the city of Richland, Washington, to Priest Rapids Dam, a distance of about 90 km (Fig. 1). The western bank of the river lies mostly within the boundaries of the U.S. Department of Energy's Hanford Site; the eastern bank is mostly privately owned land downstream from Ringold Springs. The land within the boundaries of the Hanford Site is largely undeveloped; in general, private land supports irrigated crops at places where soil conditions are favorable.

Immediately after the establishment of the Hanford Site in 1943, the Columbia River between Priest Rapids and Richland was closed to public use. Strict control was maintained until the late 1960s when the river was opened for public boating upstream to the abandoned townsite at Hanford (Fig. 1). In 1978, the entire Reach of the Columbia was opened to public boating use.

Because of long-standing restrictions to public use, the Hanford Site has acted as a refugium for wildlife in a region that is otherwise being steadily converted from sagebrush-grass ecosystems to irrigated crops. The Columbia River adjacent to the Hanford Site is the only free-flowing segment of that river in the United States upstream from Bonneville Dam. The remainder of the river is slack water created by a series of dams extending from Bonneville upstream to Grand Coulee.

[1]Work performed for the U.S. Department of Energy under Contract DE-AC06-76RLO 1830.

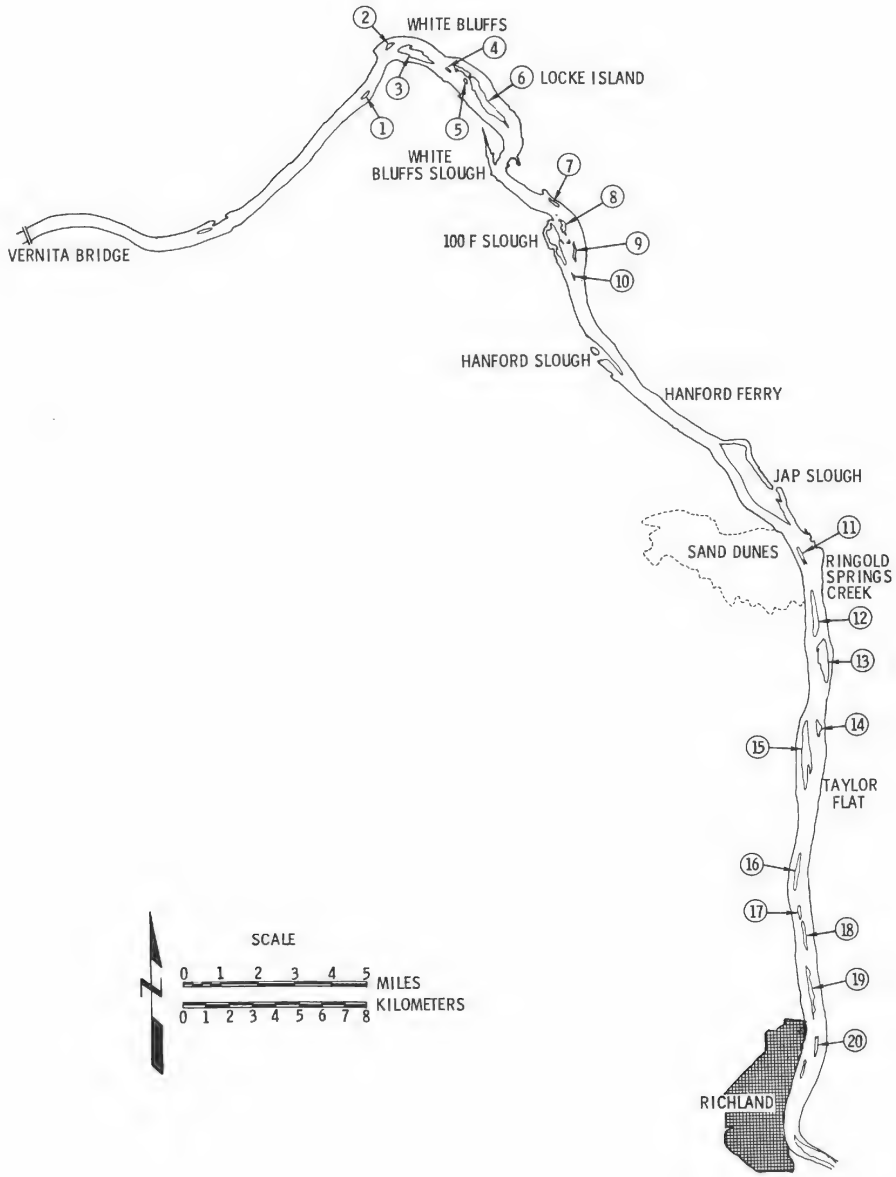


Figure 1. Hanford Reach of the Columbia River showing location of 20 islands used by nesting Canada geese.

This paper summarizes the existing information concerning the non-fisheries biological resources along the Hanford Reach of the Columbia River. Plant names are

derived from Hitchcock and Cronquist (1973), bird names from A.O.U. (1957) and A.O.U. (1973).

Plant Communities

The plant communities along the Hanford Reach of the Columbia River have not been described in the literature. Daubenmire (1970), in his monograph of the vegetation of interior Washington, provides no description of the plant communities along the Columbia. The most striking feature of Columbia River shoreline plant communities is the paucity of tree corridors, willows and cottonwoods, that characteristically border most streams and rivers. Instead, the streamside vegetation consists of a narrow zone of shrub-willows and various species mixtures of rushes, grasses, and forbs that have the capacity to become established and grow in a rooting substrate consisting mostly of water-worn cobbles and assorted gravels.

Plant community mapping of 20 small islands scattered through the Hanford Reach (done in conjunction with a study of the resident, nesting Canada goose population) has been reported by Hanson and Eberhardt (1971). A team of biologists from the University of Washington mapped the general vegetation patterns along the Hanford Reach as part of a much broader study of the inventory of wildlife along the Columbia River extending from Richland to the Canadian border (U.S. Army Corps of Engineers, 1976).

Although the Hanford Reach of the Columbia River is free-flowing, the historical seasonal and daily pulses of water-level fluctuations have been dramatically altered through storage and release of water for power generation at upstream dams. The streamside vegetation has been changing in response to these water-level fluctuations. Rooting substrates that historically were wetted once a year for a few weeks during the spring flood are now wetted almost daily. There are no baseline reference points or studies specifically established to record the influence of man-induced water fluctuations upon species composition of these streamside plant communities. A summary of the riparian plant communities associated with the Hanford Reach is shown in Table 1.

Threatened and Endangered Plants

Astragalus columbianus has been considered endangered and probably extinct by the United States Fish and Wildlife Service. However, according to Sauer *et al.* (1979), a population of *A. columbianus* occupies non-riparian habitat on benches well elevated above flood stage near Priest Rapids Dam along the western shore of the Columbia River. The population is aggressive, appears to be self-sustaining, and is not in any immediate danger of becoming extinct.

Avifauna

Birds of Prey

Bald Eagles (*Haliaeetus leucocephalus*) regularly use the Hanford Reach during fall and winter months. Employing ground observations and aerial flights, Fitzner and Hanson (1979) showed that the number of wintering Bald Eagles using the Hanford Reach has increased from about 6 birds in the 1960s to 20 birds at the present time. Eagles are attracted to the Columbia River because of salmon carcasses washed ashore from spawning beds scattered along the Hanford Reach (Watson, 1978). Although

TABLE 1. Summary of riparian plant communities associated with the Hanford Reach.

	Species	Substrate and water level fluctuations	Location	
Riparian Categories				
I	Watercress	permanently wet, little water level fluctuation daily or seasonally	Ringold Spring Creek and Seeps	WET
II	Water smartweed speedwell	frequently inundated by fluctuating water level, cobble substrate	narrow zone, all along the river	
III	Bulrush, Spike-rush, cattail	frequently wetted by fluctuating water level, cobble substrate or mud	small isolated patches along the river, cattails best developed at Ringold Springs	
IV	Reed canary grass barnyard grass goldenrod, sneezeweed, coreopsis, conyza, sweet clover, begger's tick, sandbar willow, mulberry, cottonwood, Russian olive—others	Periodically wetted by fluctuating water levels, cobble substrate	communities are best developed at Ringold Springs, Taylor Flats, Jap Slough, 100 F Slough, Hanford Slough, White Bluffs Slough	
V	Wormweed absinth, sand dropseed shrub eriogonum, lupine	wetted only in annual flood periods, cobble substrate	scattered locations along the river and island shores, 100 D gravel bar, 100 F area	
Non-Riparian Categories				
VI	Sagebrush, bitterbrush rabbitbrush, spiny hopsage, cheatgrass sandberg bluegrass, tumble mustard, tansy mustard	soil substrate, not wetted by river fluctuation even at flood stage	lands on the Hanford Site including slopes of the Ringold Bluffs	
VII	Scurf pea, pale evening primrose, thick-spike wheatgrass, sanddock	sand dunes not wetted by river fluctuation even at flood stage	sand dunes on the west bank of the river opposite Ringold Springs	DRY

Scientific plant names

Category I: **Rorippa nasturtium-aquatica** Category II: **Polygonum amphibium Veronica anagalis-aquatica** Category III: **Scirpus** spp., **Eleocharis palustris, Typha latifolia** Category IV: **Pharlaris arundinacea, Echinochloa crusgalli, Solidago** sp., **Helenium autumnale, Conyza canadensis, Coreopsis atkinsonsia, Melilotus officinalis, Bidens** sp., **Salix exigua, Populus deltoides** (?), **Eleagnus angustifolia, Morus alba** Category V: **Artemisia absinthium, Sporobolus cryptandrus, Eriogonum douglasii, Lupinus** sp. Category VI: **Artemisia tridentata, Purshia tridentata, Chrysothamnus nauseosus, Atriplex spinosa, Bromus tectorum, Poa sandbergii, Sisymbrium altissimum, Descurainia pinnata** Category VIII; **Psoralea lanceolata, Oenothera pallida, Agropyron dasystachyum, Rumex venosus**

salmon carcasses provide an important dietary item, eagles also prey upon disabled waterfowl. Salmon would not spawn here if the water were not flowing fast enough to provide the habitat requirements needed to promote egg hatching and food for juvenile salmon.

The Hanford population of wintering eagles is small compared to wintering populations in western Washington. The Nooksack River population is estimated at 100 birds (Stalmaster *et al.* 1978). In the absence of human harassment, Bald Eagles will probably continue to use the Hanford Reach so long as salmon carcasses remain available as a food source.

The American Osprey (*Pandion haliaetus*) occasionally fishes along the Columbia River, but there are no nesting pairs, possibly because of the lack of suitable nesting trees. Nesting birds of prey have been intensively studied on the Hanford Site (Fitzner *et al.*, 1980). Nests of Swainson's Hawks (*Buteo swainsonii*), Red-tailed Hawks (*Buteo jamaicaensis*), Prairie Falcon (*Falco mexicanus*), and American Kestrel (*Falco sparverius*) are located along the Columbia River; however, the food of these birds is mostly of terrestrial origin and shows little alliance to the Columbia River. The Marsh Hawk (*Circus cyaneus*) is present year around and can often be seen flying low along the edge of the river and hovering over riparian plant communities. This hawk also nests on islands in the Columbia River. Great Horned Owls (*Bubo virginianus*) and Common Ravens (*Corvus corax*) occasionally nest on the steep bluffs. Long-eared (*Asio otus*), and Great Horned Owls have been observed nesting in the few scattered trees along the Columbia River, mainly from Hanford ferry crossing upstream for about 10 km on the western shore.

Geese and Ducks

The resident Great Basin Canada Goose (*Branta canadensis moffitti*) population on the Hanford Reach has been regularly censused since 1950 (Hanson and Browning, 1959; Hanson and Eberhardt, 1971; Rickard and Sweany, 1977). Nesting has been almost entirely confined to twenty islands scattered throughout the Hanford Reach (Fig. 1), with less than 1 percent of the nests located on the sand and clay cliffs bordering the river on the east. The number of goose nests established on these islands has fluctuated from year to year, but overall there has been a general decline in numbers (Fig. 2). As many as 300 goose nests were present in the early 1950s; however, in 1976 only 77 nests were located on these islands. One of the main reasons for the marked decline in goose nests is predation by coyotes. Predation has occurred from time to time on most of the islands, but resident coyotes have totally discouraged goose nesting on Island 6 (Locke Island), which formerly supported 100 nests (Fig. 2).

The Hanford goose nesting population is the largest along the Columbia River, although there are nesting populations located both upstream and downstream from the Hanford Site. Gibson and Buss (1977) report that the creation of slack water behind a series of dams along the lower Snake River has all but eliminated the nesting population from that section of the Snake River. Nevertheless, a few geese still nest on ledges of steep basalt cliffs along the impoundments. A few Mallards (*Anas platyrhynchos*) also nest along the Columbia River (Hanson and Eberhardt, 1971).

Migrant ducks and geese including Blue (*Chen coerulescens*) and Snow geese (*C. hyperborea*) have historically used the Hanford Reach as a resting stop in fall and winter. They make foraging flights to surrounding fields and rest on the islands and water at other times. During the early years when the river was closed to public use, as many as 250,000 ducks and geese used the river. Since the opening of the river to public boating and recreational hunting from the Hanford townsite downstream to Richland, only about 100,000 waterfowl rest on this section of the river. Major waterfowl concentrations are located immediately above the Hanford townsite in the no hunting area and on lakes and ponds located on the nearby Saddle Mountain Wildlife Refuge. During the late 1950s and early 1960s when reactor effluent waters entered the Columbia River, radioactive phosphorus and radioactive zinc were readily detected

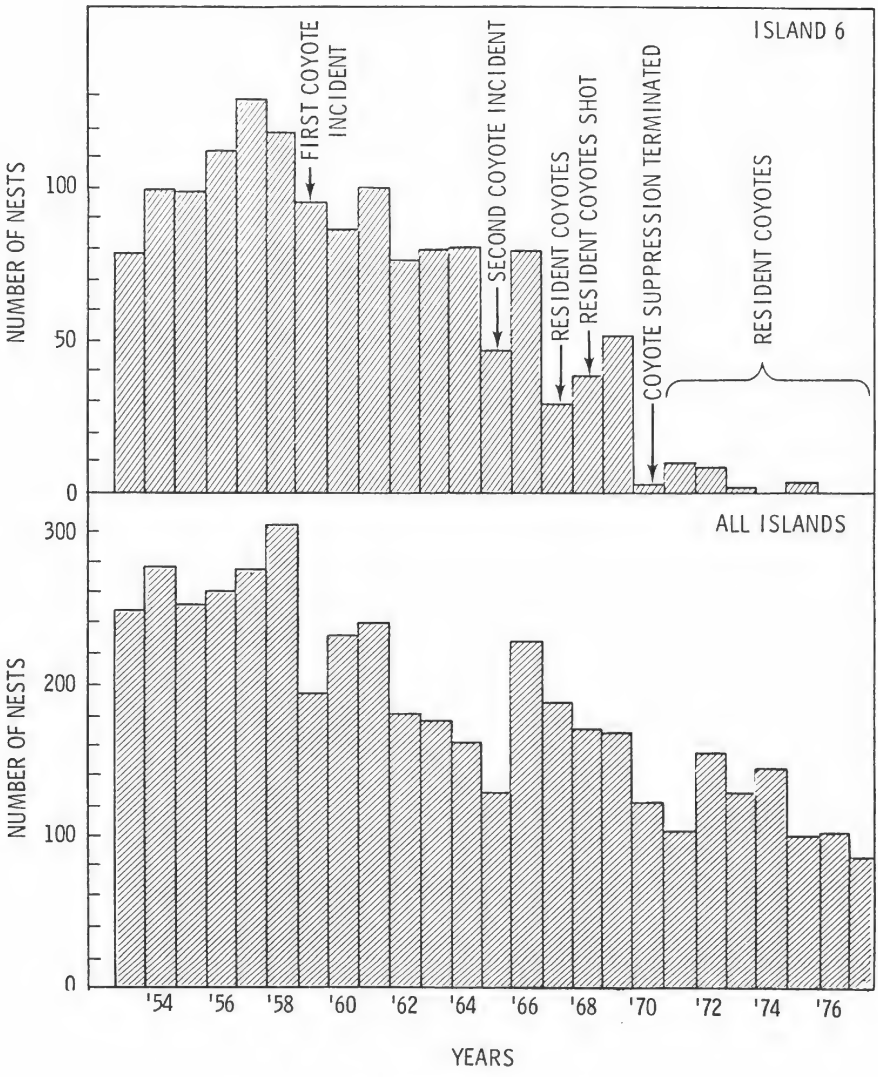


Figure 2. Number of Canada goose nests established on Columbia River islands 1953-1977.

in the bodies of Mallard, Pintail (*A. acuta*), teal, and other ducks that wintered along the Columbia (Hanson and Case, 1963). Since the shutdown of the old style single pass reactors in the late 1960s, there has been no radiophosphorus or radiozinc in the river water even though one production reactor remains operational.

Members of the Lower Columbia Basin Audubon Society regularly census wintering populations of waterfowl along the Columbia River near Richland during the annual Christmas bird counts. Species lists are published in American Birds (1978).

Fish-eating Birds

In the 1950s and 1960s Ring-billed (*Larus delawarensis*) and California (*L. californicus*) gulls nested on Island 1 near Coyote Rapids and on Island 12 near Ringold Springs (Hanson, 1963). However, in the early 1970s gulls abandoned these islands, and colonies are now present on Islands 18 and 20 near the city of Richland (Fig. 1). Recent nesting population surveys show that approximately 5250 California gull pairs and 5100 Ring-billed gull pairs nest on the two islands. About 8450 young gulls were banded with Fish and Wildlife Service metal leg bands during the years 1956 through 1970 by W. C. Hanson and associates. Preliminary analyses of band returns indicate that Hanford gulls move westward to the Pacific coast and northward into British Columbia during their first migration flights. Subsequent band recoveries have mostly been reported from the coastal areas of California and Mexico, with scattered reports from inland areas of the western U.S. Forster's terns (*Sterna forsteri*) also nest on Islands 18, 19, and 20 on bare cobblestone substrate close to the waterline. Fluctuations in water level, caused by upstream dams, sometimes inundate nests. We estimate that about 400 pairs of these terns nest along the Hanford Reach of the Columbia River.

A colony of double-crested cormorants (*Phalacrocorax auritus albaciatus*), estimated at 55 to 65 birds, nested on Locke Island during the mid-1950s (Hanson, 1968). This colony was abandoned in 1957 because of the intense competition with Great Blue Herons for nesting sites in a few low-statured mulberry trees. Occasionally a few birds have been seen on the Columbia River between Richland and Ringold Springs in winter. In the years 1950 through 1967, 15 to 20 White Pelicans (*Pelicanus erythrorhynchos*) regularly used the Hanford Reach as a foraging stop in migration. In 1979 the number had dwindled to less than 10. A few American Mergansers (*Mergus merganser*) also nest along the Columbia River. Great Blue and Black-crowned Night (*Nyctocorax nycticorax*) herons have nested along the Columbia River for many years. Hanson (1968) noted a small colony on Locke Island that contained 10 to 16 nests of each species during the 1950s. The number of Great Blue Herons using the Columbia River has increased in recent years. At present about 40 pairs nest in a grove of trees near the White Bluffs ferry landing. Nesting colonies are widely scattered in interior Washington probably because of the scarcity of suitable trees. A large mixed colony of about a thousand Great Blue and Black-crowned Night herons has recently become established in peach leaf willow trees (*Salix amygdaloides*) on the northern extremity of the Potholes Reservoir in Grant Co. (Fitzner *et al.*, 1978). Another colony of Great Blue Herons is located on the Umatilla Wildlife Refuge along the Columbia River near Umatilla, Oregon.

Upland Game Birds

Small breeding populations of California Quail (*Lophortyx californicus*) and Ring-necked Pheasants (*Phasianus colchicus*) occur along the river, especially in the shrub willows and remnants of abandoned orchards. These birds are not subjected to hunting pressure, but a few birds are killed each year for radiological surveillance purposes (Houston and Blumer, 1979). There are larger pheasant populations associated with the irrigated farmlands surrounding the Hanford Site. Quail populations are much larger in the brushy draws and ravines along the Snake River canyon and in the foothills of the Blue Mountains. Sage Grouse (*Centrocercus urophasianus*) formerly occupied habitats in the southern and western parts of the Hanford Site, gradually disappearing

by the mid-1960s. A few Sage Grouse persist in the Rattlesnake Hills. A single covey of Scaled Quail (*Callipepla squamata*) was noted on the Wahluke slope in 1956. They have not been observed since.

In spring, Mourning Doves (*Zenaida macroura*) nest in the dryland habitats bordering the Columbia River and on the islands. Some doves winter in this area.

Shorebirds

The Long-billed Curlew (*Numenius americanus*) nests on the Hanford Site in dry sagebrush vegetation. The nesting birds apparently avoid streamside shrub-grass communities. However, birds that are produced on the Hanford Site congregate on islands in the Columbia just before the onset of autumn migration (Allen, 1980). Another, larger curlew population breeds in sagebrush-grass vegetation near Boardman, Morrow Co., Oregon.

Lists of shorebird species that occur along the Columbia River appear in North American Birds (1978). Although the shorebird habitat is likely to be affected by fluctuating water levels, there has been no consideration of the response of shorebirds to such changes.

Other Birds

There have been no studies specifically designed to census the bird populations associated with shoreline tree/shrub communities of the Hanford Reach. However, bird surveys have been conducted in riparian communities with similar plant species composition and general structural appearance on the Hanford Site (Rotenberry *et al.*, 1979) (Table 2) and along the Snake River canyon (Lewke and Buss, 1977). Fitzner and Rickard (1977) surveyed birds in riparian communities associated with waste ponds on the Hanford Site, and winter bird populations have been censused in tree communities along the Yakima River flood plain at Richland, Washington (Rickard and Rickard, 1972). Although similar bird species composition can be expected in Columbia River tree/shrub communities as in other tree/shrub riparian communities, more accurate counts are needed to estimate bird utilization of Columbia River shoreline communities.

Mammals

Deer

The mule deer (*Odocoileus hemionus*) is the most numerous big game animal on the Hanford Site. The islands and riparian plant communities along the Hanford Reach of the Columbia provide fawning habitat. Current information concerning the known information about Hanford deer has been summarized by Eberhardt *et al.* (1979). Hedlund (1957) reported that mule deer tagged as fawns were hunter-killed at points as far as 110 km from their point of capture (Fig. 3). A few deer are killed each year by automobiles on Hanford Site highways, and samples of tissues are taken for radiological surveillance purposes (Houston and Blumer, 1979).

The existence of the mule deer population at Hanford hinges upon two important factors: first, hunting is not permitted, thus protecting the deer population from seasonal harvest and from poaching mortality; second, the land use of the Hanford Site is non-agricultural, which allows the deer to forage without incurring crop damage claims by land owners, thus encouraging the Washington Game Department to keep the

TABLE 2. Most abundant birds recorded in a riparian tree-shrub community on the Arid Lands Ecology Reserve. (Modified from Rotenberry **et al.**, 1979).

Breeding birds			Wintering birds		
Mourning Dove	28.5	(11)	Dark-eyed Junco	26.5	(9)
Zenaida macroura			**Junco hymenalis**		
Chukar	20.7	(7)	Yellow-rumped Warbler	4.7	(2)
Alectoris chukar			**Dendroica coronata**		
Western Meadowlark	19.4	(11)	Western Meadowlark	3.7	(5)
Sturnella neglecta			**Sturnella neglecta**		
Barn Swallow	8.9	**(11)**	American Robin	2.6	(6)
Hirundo rustica			**Turdus migratorius**		
Northern Oriole	7.6	(10)	Black-billed Magpie	2.2	(8)
Icterus galbula			**Pica pica**		
Vesper Sparrow	7.4	(7)	White-crowned Sparrow	1.8	(5)
Pooecetes gramineus			**Zonotrichia leucophrys**		
Starling	5.6	(5)	Ring-necked Pheasant	1.7	(5)
Sturnus vulgaris			**Phasianus colchicus**		
Lazuli Bunting	5.5	(10)	Song Sparrow	1.6	(7)
Passerina amoena			**Melospiza melodia**		
Black-billed Magpie	5.2	(10)	California Quail	1.5	(1)
Pica pica			**Lophortyx californicus**		
Wilsons' Warbler	3.7	(4)	Ruby-crowned Kinglet	1.2	(6)
Wilsonia pusilla			**Regulus calendula**		
Brewers' Blackbird	2.8	(6)	20 Other species	10.2	
Euphagus cyanocephalus					
Eastern Kingbird	1.9	(5)			
Tyrannus tyronnus					
California Quail	1.8	(6)			
Lophortyx californicus					
Western Tanager	1.5	(5)			
Piranga lusdoviciana					
Song Sparrow	1.4	**(7)**			
Melospiza melodia					
Sage Grouse	1.4	**(2)**			
Centrocercus urophasianus					
Yellow-breasted Chat	1.1	(6)			
Icteria virens					
Brown-headed Cowbird	1.1	(3)			
Molothrus ater					
White-crowned Sparrow	1.0	**(1)**			
Zonotrichia leucophrys					
American Kestrel	1.0	**(7)**			
Falco sparverius					
Rock Wren	1.0	(7)			
Salpinctes vulgaris					
38 Other species	12.1				

The tree-shrub community consists of a narrow corridor of cottonwood and willow trees about 1.5 km long and usually less than 30 meters across. Other species: Golden Eagle, Red-tailed Hawk, Goshawk, Cooper's Hawk, Rough-legged Hawk, Swainson's Hawk, Pigeon Hawk, Long-eared Owl, Common Raven, Loggerhead Shrike, Northern Shrike, Killdeer, Red-winged Blackbird, Tree Swallow, Night Hawk, Black-headed Grosbeak, Vesper Sparrow, Savannah Sparrow, Lark Sparrow, Rufous-sided Towhee, Sage Sparrow, Golden-crowned Sparrow, Slate-colored Junco, Western Kingbird, Say's Phoebe, Trails' Flycatcher, Western Wood Pewee, Dusky Flycatcher, Rock Wren, Canyon Wren, Winter Wren, House Wren, Long-billed Marsh Wren, Red-shafted Flicker, Golden-crowned Kinglet, Red-eyed Vireo, Warbling Vireo, Solitary Vireo, Nashville Warbler, Yellow Warbler, Townsend's Warbler, McGillray's Warbler, Varied Thrush, Hermit Thrush, Townsend Solitaire, Rufous Hummingbird.

Values are average number of individuals seen in 11 breeding seasons (May-August) and in 10 wintering seasons (November-March) counts. Actual count in which each species was observed is in parentheses.

herd size as small as practical. The Hanford mule deer population is isolated from larger deer populations in the Blue Mountains to the east, the Cascade Mountains to the west, and from the Snake River canyon population by many miles of intervening farmland. A few mule deer reside in the Rattlesnake Hills, but no one knows whether this small population is isolated from the larger deer population along the Columbia River.

The mule deer herd on the Hanford Site may not be as healthy as other populations. Steigers (1978) stated that the daily movements of radiotelemetered fawns on the Hanford Site were greater than those of fawns at other locations. This finding may be an indication that parent deer have to travel farther to obtain their daily dietary

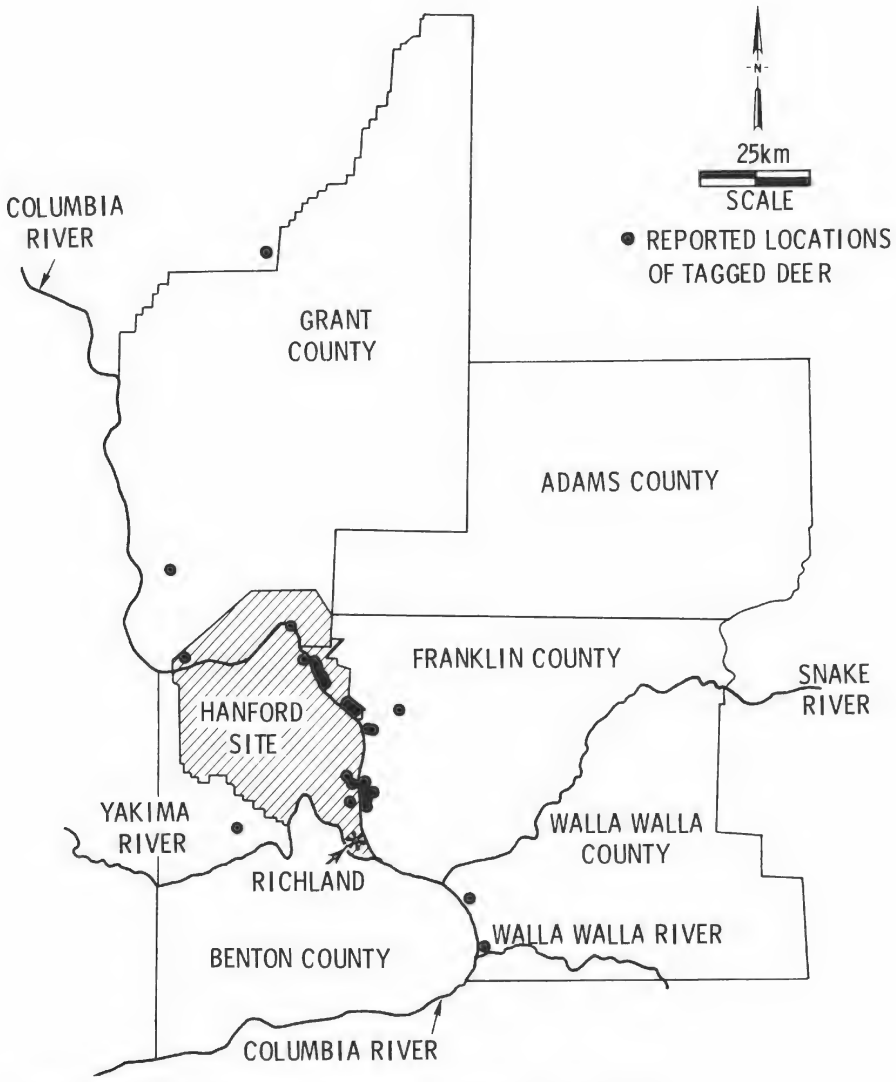


Figure 3. Recovery locations of mule deer tagged on the Hanford Site.

requirements. Eberhardt *et al.* (1979) examined six years of fawn tagging records from the Hanford Site. These data showed a decline in the number of fawns tagged in the last three years of record, suggesting that fewer fawns were being produced. Perhaps there are fewer females to produce fawns, or fawn predation has become more pronounced, or fawning occurs elsewhere. Tagging was conducted primarily on islands, and this may have disturbed the deer; as a result, fawning may have moved inland.

Apparently summer browse plants on the Hanford Site are scarce, and the few

available trees are being utilized to their maximum. Inadequate summer browse might contribute to a decline in the general health and productivity of a deer population. However, there is no information concerning total numbers, sex ratios, average weights, or age distribution of the Hanford mule deer herd.

The most conspicuous plants along the Hanford Reach of the Columbia River are a few aged trees (shade and ornamentals) planted around farmsteads in the years prior to 1943. These are mostly Chinese elm (*Ulmus* sp.), black locust (*Robinia pseudacacia*), lombardy poplar (*Populus* sp.), white poplar (*Populus alba*), eastern cottonwood (*Populus* sp.), and mulberry (*Morus* sp.). At a few places some fruit trees still survive, especially apricots. Over the years some of these trees have died and have been uprooted or broken by strong winds.

Mulberry, Russian olive, cottonwood, and peach-leaf willow are aggressive enough to establish seedlings at favorable microsites in the riparian zone (Fig. 4). Tree foliage

Figure 4. Trees self-established in the riparian zone.

provides a forage source for mule deer and porcupine (*Erethizon dorsatum*). Mule deer eat leaves hanging within their reach. Trees provide pools of shade which are actively sought by mule deer during the hot, sunny summer months. Nearly all of the trees along the western bank of the Columbia River show browse-lines by deer (Fig. 5). Since most of the deer population is confined to the western shore under the protective umbrella provided by the Hanford Site, volunteer mulberry trees on the western shore are severely pruned by mule deer while those on the opposite shore remain relatively untouched. Occasionally a white-tailed deer (*Odocoileus virginianus*) is observed on the Hanford Site (O'Farrell and Hedlund, 1972).

Furbearers

Coyotes (*Canis latrans*) are important predators of mule deer fawns on the Hanford Site (Steigers, 1977). Although the Columbia River is not an impossible barrier to coyote movement, radiotracking studies showed that tagged coyotes spent a great deal of their time within a distance of a few kilometers of the river (Springer, 1977). The coyote population is probably greater on the Hanford Site than on the surrounding farmlands. About 700 coyotes were removed from Hanford and surrounding environs each year during the period 1950 to 1970 by the U.S. Fish and Wildlife Service (Hanson and Eberhardt, 1971). Coyote trapping is practiced as a source of income and as a recreational endeavor around the periphery of the Hanford Site.

Beaver (*Castor canadensis*), muskrat (*Ondatra zibethica*), and mink (*Mustela vison*) occur along the Columbia River. There is no estimate of their abundance. The most suitable slack water habitats are in the vicinity of Ringold Springs, Jap slough, Hanford slough, 100F slough, and White Bluff slough (Fig. 1). Other furbearing

Figure 5. Trees showing browse lines created by mule deer.

mammals that occur along the river but for which there is no specific information are raccoon (*Procyon lotor*), skunk (*Mephitis mephitis*), weasels (*Mustela frenata* and *M. erminea*), and bobcat (*Lynx rufus*).

Small Mammals

Small mammals undoubtedly occur in the riparian plant communities along the shore of the Columbia River, although there have been no specific studies made on species composition or relative abundance. Deer mice (*Peromyscus maniculatus*), house mice (*Mus musculus*), vagrant shrew (*Sorex vagrans*), and montane meadow mouse (*Microtus montanus*) are present. The Columbia River is well known as a barrier to the dispersal of Ord's kangaroo rat (*Dipodomys ordii*) and the Washington ground squirrel (*Spermophilus washingtoni*): both of these species occur on the east bank of the river but not on the west bank. Preliminary data indicate that some of the islands do harbor these species. Bushytail woodrats (*Neotoma cinerea*) occur in abandoned buildings and in trees planted by homesteaders.

Hares and Rabbits

Black-tailed hares (*Lepus californicus*) occur throughout the undeveloped sagebrush-grass vegetation along the Columbia River, but these animals are not dependent upon riparian vegetation for their existence. However, cottontails (*Sylvilagus nuttallii*) seem to prefer edge habitats where riparian tree/shrub communities adjoin sagebrush-grass communities. There have been no studies made to estimate the abundance of cottontails along the Hanford Reach.

Ecological Relationships

Prey/Predator Relationships

Coyotes have been instrumental in the observed decline in the nesting Canada Goose population. Coyotes destroy nests, occasionally kill adult geese, and have made Locke Island unacceptable for nesting. Coyotes are also an important cause of mule deer fawn mortality and also contribute to destruction of nests of the Long-billed Curlew (Fitzner, 1978). The coyote is an extremely versatile predator. A few individuals have learned to capture live fish, mostly carp, trapped in shallow pools along the shoreline of the Columbia (Springer, 1980).

The Great Blue Heron colony at White Bluffs depends upon fish as a food source during the nesting season. Trash fish, carp and suckers, are probably the most important food items. The Bald Eagles depend primarily upon the annual run of anadromous fish to provide winter food in the form of salmon carcasses.

Large numbers of Cliff (*Petrochelidon pyrrhonata*) and Bank swallows (*Riparia riparia*) nest on the steep cliffs bordering the east bank of the river. These birds catch flying aquatic insects, especially caddis flies, that emerge from the riffle substrates of the Columbia River in large numbers in spring and summer months. Some swallows, adult and young, are the prey of Prairie Falcons and American Kestrels that nest on shelves and in cavities on the same cliffs.

Food Chains and Chemical Contamination

High trophic level animals characteristically have low population densities and also have low reproductive potential. Populations of some of these animals, particularly

raptorial birds such as the Bald Eagle and Peregrine Falcon, have declined to the extent that they are regarded as "endangered" or "threatened." Because high trophic level animals are often wary and are not abundant, ways other than killing need to be devised to determine whether chemical contaminants are transmitted to them through their diets. Rickard *et al.* (1977) collected detritus cast from heron nests as an indicator of radionuclide contamination in heron foods. Springer (1977) collected coyote scats from various parts of the Hanford Site as indicators of radionuclides in coyote foods. Fitzner *et al.* (1980) collected the regurgitated pellets from nest sites and roosts of hawks and owls on the Hanford Site. Radiochemical analyses of these pellets indicated that some of these birds had access to prey items containing radionuclides of Hanford origin. The use of fecal materials and castings appears to be a useful way to monitor high trophic level animals in order to detect buildups of persistent chemicals in their environments. This method of monitoring would be especially useful in pristine and other environments that maintain enough of their essential ingredients to support populations of high trophic level animals.

Literature Cited

Allen, Julia N. 1980. The Ecology and Behavior of the Long-billed Curlew, *Numenius americanus parvus*, in Southeastern Washington. Wildl. Monograph, August.

American Birds. 1978. Seventy-eighth Christmas bird count, Vol. 32. No. 4. National Audubon Society, Inc., New York.

American Ornithologists Union. 1957. Check-list of North American birds. Fifth Edition. Port City Press, Baltimore.

———. 1973. Thirty-second supplement to the American Ornithologists' Union check-list of North American birds. Auk 90:411-419.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Washington State Univ. Agr. Expt. Sta. Tech. Bull. 62.

Eberhardt, L. E., J. D. Hedlund, and W. H. Rickard. 1979. Tagging studies of mule deer fawns on The Hanford Site, 1969-1977. PNL-3147, Pacific Northwest Laboratory, Richland, Wash.

Fitzner, R. E., W. H. Rickard, L. L. Cadwell, and L. E. Rogers. 1980. Raptors of the Hanford Site. PNL-3212, Pacific Northwest Laboratory, Richland, Wash.

———, and ———. 1975. Avifauna of waste ponds, ERDA Hanford Reservation, Benton County, Washington. BNWL-1885, Pacific Northwest Laboratory, Richland, Wash.

———, D. F. Martin, and R. E. Frieze. 1978. First breeding record for the Great Egret (*Casmerodius albus*) in Washington. Murrelet 60:33-34.

———, and W. C. Hanson. 1979. Wintering Bald Eagles along the Columbia River in southcentral Washington. Condor 81:311-313.

Gibson, L. W., and I. O. Buss. 1977. Reactions of Canada Geese to reservoir impoundment of the Snake River in Washington. Northw. Sci. 46:301-318.

Hanson, W. C., and R. L. Browning. 1959. Nesting studies of Canada Geese of the Hanford Reservation 1953-1956. J. Wildl. Manage 23:129-137.

———. 1963. Census of Ring-billed and California gulls in eastern Washington. Condor 65: 163-164.

———. 1968. Recent history of Double-crested Cormorant colonies in southeastern Washington. Murrelet 49:25-26.

———. 1969. First sight records of Blue Geese in Washington. Murrelet 50:24.

———, and L. L. Eberhardt. 1971. A Columbia River Canada Goose Population. Wildl. Monograph No. 28.

———, and A. C. Case. 1963. A method for measuring waterfowl dispersion utilizing phosphorus-32 and zinc-65, pp. 451-453 *in* V. Schultz and A. W. Klement (eds.), Radioecology. Reinhold, New York, and Am. Inst. of Biol. Sci., Washington, D.C.

Hedlund, J. D. 1975. Tagging mule deer fawns in southcentral Washington. Northw. Sci. 49:153-157.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. of Wash. Press.

Houston, J. R., and P. J. Blumer. 1979. Environmental status of the Hanford Site for CY 1978. PNL-2933, Pacific Northwest Laboratory, Richland, Wash.

Lewke, R. E., and I. O. Buss. 1977. Impacts of impoundments to vertebrate animals and their habitats in the Snake River canyon, Washington. Northw. Sci. 51:219-270.

O'Farrell, T. P., and J. D. Hedlund. 1972. White-tailed deer, *Odocoileus virginianus*, in southcentral Washington. J. Mammal. 53:907-909.

Rickard, W. H., and B. J. Rickard. 1972. A comparison of winter bird populations after a decade. Murrelet 53:42-47.
———, J. D. Hedlund, and R. G. Schreckhise. 1977. Rejecta cast from heron nests an an indicator of environmental contamination. Auk 95:425-427.
———, and H. A. Sweany. 1977. Radionuclides in Canada Goose eggs, pp. 623-628 *in* Biological Implications of Metals in the Environment. Conf.-750929, TIC, Oakridge, Tenn.
Rotenberry, J. T., R. E. Fitzner, and W. H. Rickard. 1979. Seasonal variation in avian community structure; differences in mechanisms regulating diversity. Auk 96:499-505.
Sauer, R. H., J. Mastroguiseppe, and R. Smookler. 1979. *Astragalus columbianus* Barneby: Rediscovery of an "extinct species." Brittonia 31:261-264.
Springer, J. T. 1977. Movement Patterns of Coyotes in Southcentral Washington as Determined by Radiotelemetry. Wash. State Univ., Pullman, Ph.D. thesis.
———. 1979. ^{90}Cr and ^{137}Cs in coyote scats from the Hanford Reservation. Health Physics 36: 31-33.
———. 1980. Fishing behavior of coyotes in the Columbia River southcentral Washington. J. of Mammalogy. 62:373-374.
Stalmaster, M. V., J. R. Newman, and A. J. Hansen. 1978. Population dynamics of wintering Bald Eagles on the Nooksack River, Washington. Northw. Sci. 53:126-131.
Steigers, W. D., Jr. 1978. Mortality of Mule Deer Fawns in Southcentral Washington. Brigham Young Univ., Provo, Utah, M.S. thesis.
U.S. Army Corps of Engineers, North Pacific Division. 1976. Inventory of Wildlife Habitat and Associated Wildlife along Columbia and Snake Rivers. Vol. IV-A and Vol. IV-B Mid-Columbia River.
Watson, D. G. 1978. Fall chinook salmon spawning near Hanford, 1976, *in* Pacific Northwest Laboratory Annual Report for 1977, PNL-2500, pt. 2, Pacific Northwest Laboratory, Richland, Wash.

Received May 2, 1980
Accepted for publication June 23, 1980

Association News

The 55th Annual Meeting of the Northwest Scientific Association was held at Walla Walla College on 17-19 March. The meeting included a symposium on Biotelemetry and Radio Tracking. The Association enjoyed a superbly illustrated banquet speech by Dr. Robert J. Carson on "Mt. St. Helens: Past and Present." One hundred twenty-four papers were presented in the symposium and the following sections: Botany, Chemistry/ Mathematics, Forestry, Geology, Social Science, Soil and Water, and Zoology. Copies of the Program and Abstracts are available from the treasurer at cost ($3).

Dr. Phil Haddock, Professor Emeritus, University of British Columbia, was named an Honorary Life Member by the Association in recognition of his scientific contributions, especially in the area of preservation of natural areas. Research grant awards were given to Arlene T. Doyle, Department of Zoology, Oregon State University; Dennis G. Joyce, Forest Resources Department, University of Idaho; and David R. Polivka, Earth Sciences Department, Portland State University.

The new officers of the Association are: President, John Perkins; and Vice President, Steven F. Arno. Six new Trustees were elected to the Board. They are Alan Black, T. A. (Andy) Black, Roger del Moral, Thomas Nimlos, Steven R. Seavy, and Kareen Sturgeon.

The tentative meeting dates for the 1983 annual meeting at The Evergreen State College are 24-26 March.

Robert L. Carr
Secretary

The following reprint and page charges for Northwest Science will be effective for all papers printed after 1 January 1982:

No. printed pages	1-4	5-8	9-12	13-16	17-20
Cost per 100 copies	$39	$52	$69	$71.50	$84.50

Page charges will increase to $50 per page.

In addition, the Trustees and Members approved an increase of individual and institutional memberships for 1982. Regular memberships will be $14 and student membership will be $8.

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian D. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Andrew V. Corry
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
F. A. Gilfillan
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
Maurice T. James
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Frank D. Nicol
William A. Rockie
Francis J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
S. C. Vandecaveye
Richard B. Walker
D. J. Wort

1982 Sustaining Institutional Members

Battelle Northwest, Richland, WA
MacMillan Bloedel, Ltd., Nanaimo, B.C. Canada
Potlatch Corporation, Lewiston, ID
The Washington Water Power Company, Spokane, WA
Weyerhaeuser Company, Centralia, WA

1982 Institutional Members

Boise State University, Boise, ID
British Columbia Institute of Technology, Burnaby, B.C. Canada
Central Oregon Community College, Bend, OR
Central Washington University, Ellensburg, WA
Centralia College, Centralia, WA
College of Idaho, Caldwell, ID
Eastern Montana College, Billings, MT
Eastern Oregon State College, LaGrande, OR
Eastern Washington University, Cheney, WA
Edmonds Community College, Lynwood, WA
The Evergreen State College, Olympia, WA
George Fox College, Newberg, OR
Gonzaga University, Spokane, WA
Grays Harbor College, Aberdeen, WA
Green River Community College, Auburn, WA
Highline Community College, Midway, WA
Idaho State University, Pocatello, ID
Lewis-Clark State College, Lewiston, ID
Lewis and Clark College, Portland, OR
Linfield College, McMinnville, OR
Malaspina College, Nanaimo, B.C. Canada
Montana College of Mineral Science and Technology, Butte, MT
Mt. Hood Community College, Gresham, OR
North Idaho College, Coeur d'Alene, ID
Northern Montana College, Havre, MT
Oregon College of Education, Monmouth, OR
Oregon Institute of Technology, Klamath Falls, OR
Oregon State University, Corvallis, OR
Pacific Lutheran University, Tacoma, WA
Pacific University, Forest Grove, OR
Peninsula College, Port Angeles, WA
Portland State University, Portland, OR
Saint Martin's College, Lacey, WA
Seattle Central Community College, Seattle WA
Seattle Pacific University, Seattle, WA
Shoreline Community College, Seattle, WA
South Seattle Community College, Seattle, WA
Southern Oregon State College, Ashland, OR
Southwestern Oregon Community College, Coos Bay, OR
Spokane Falls Community College, Spokane, WA
University of Idaho, Moscow, ID
University of Montana, Missoula, MT
University of Oregon, Eugene, OR
University of Puget Sound, Tacoma, WA
University of Victoria, Victoria, B.C. Canada
University of Washington, Seattle, WA
Walla Walla College, College Place, WA
Washington State University, Pullman, WA
Western Washington University, Bellingham, WA
Whitman College, Walla Walla, WA
Yakima Valley College, Yakima, WA

1982 Sustaining Individual Members

Donald J. Brown, Richland, WA
Randall E. Brown, Pasco, WA
Susan G. Conard, Corvallis, OR
George W. Douglas, Victoria, B.C. Canada
Bruce Ettling, Vancouver, WA
George R. Fahnestock, Seattle, WA
Gerald H. Haddock, Wheaton, IL
Frederick C. Hall, Portland, OR
Charles R. Hatch, Moscow, ID
Robert J. Jonas, Pullman, WA
Barry L. Keller, Pocatello, ID
Denis L. Lavender, Corvallis, OR
William L. Lester, Arcata, CA
William A. Long, Crescent City, CA
Albert L. Merkel, Moscow, ID
Daniel F. Milam, Bellevue, WA
Emmett B. Moore, Jr., Richland, WA
Milton M. Mosher, Pullman, WA
William A. Rickard, Richland, WA
Lee E. Rogers, Richland, WA
Raymond A. Soltero, Cheney, WA
Ronald J. Taylor, Bellingham, WA
Daniel W. Uresk, Rapid City, SD
Shepard M. Zedaker, Christiansburg, VA

NON PROFIT ORG.
U. S. Postage
PAID
Pullman, Wash.
Permit No. 1

Northwest Science

Washington State University

Pullman, Washington 99164

Willis B. Merriam
SE 420 Derby
Pullman, WA 99163

Associate Editors

Botany	Kenneth C. Swedberg	Eastern Washington University
Forestry	Arthur R. Tiedemann	U.S. Forest Service
Geology	Franklin F. Foit, Jr.	Washington State University
Soils	Stanley P. Gessel	University of Washington
Zoology	Irven O. Buss	Washington State University

Change of Address Send change of address notice to the Treasurer as listed on the inside front cover.

Instructions to Authors The pages of Northwest Science are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. At least one of the authors of papers submitted for publication must be a member of the Northwest Scientific Association. Manuscripts (original typescript plus two copies) should be submitted to the Editor, Northwest Science, Washington State University, Pullman, Washington. Prior to submitting manuscripts, authors should request a copy of "Instructions to Authors" from the Editor.

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164, U.S.A.

Volume 56, Number 2

May 1982

Northwest Science

79 Wintering Bald Eagles in Jackson Hole, Wyoming
Dennis R. Davenport and John L. Weaver

83 Nitrate and Ammonium Levels in Relation to Site Quality in Douglas-fir Soil and Litter
Daniel J. Vogt and Robert L. Edmonds

90 Bouguer Gravity Study of Enumclaw/Pinnacle Peak, Washington
Duncan S. Campbell and Daniel J. Johnson

101 Insects and Other Factors Affecting Noble Fir Seed Production at Two Sites in Oregon
J. H. Scurlock, R. G. Mitchell, and K. K. Ching

108 Numerical Phenetic Analysis of Variation in Populations of **Poa secunda** Presl. and **Bromus japonicus** Thunb. **(Poaceae)**
Bonnie Heidel, E. Jennifer Christy, and Amy Jean Gilmartin

121 The Relationship of Maximum Canopy Leaf Area to Forest Growth in Eastern Washington
Paul E. Schroeder, Brooks McCandish, Richard H. Waring, and David A. Perry

131 Opportunistic Feeding by Coyotes
Dirk Van Vuren and Stephen E. Thompson, Jr.

136 A Study of Surface Waters and Sediments in Southern Spokane County, Washington, for the Presence of **Yersinia enterocolitica**
Marion Bacon

138 Diets and Habitats of Mule Deer in South-central Washington
Daniel W. Uresk and Virginia A. Uresk

148 Inter- and Intrastream Migration of Cutthroat Trout **(Salmo clarki)** in Spawn Creek, a Tributary of the Logan River, Utah
David R. Bernard and Eugene K. Israelsen

Official Publication of the Northwest Scientific Association

US ISSN 0029 344X

Northwest Science

Volume 56, Number 2, May 1982

The Northwest Scientific Association is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to Northwest Science, is open to individual persons for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 3000 students or more, $40. All other subscribers, $20 per year. Sustaining membership, $25 per year for individual persons and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Payment should be made to the Treasurer.

Editor **John W. Weber**
Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164-2910

Officers of the Association

President **John H. Perkins**
The Evergreen State College
Olympia, Washington (1983)

Vice-President **Stephen F. Arno**
USDA Forest Service
Missoula, Montana (1983)

Secretary **Robert L. Carr**
Eastern Washington University
Cheney, Washington (1984)

Treasurer **Robert J. Jonas**
Department of Zoology
Washington State University
Pullman, Washington 99164-4220
(1983)

Past President **James R. Chambers**
Walla Walla College
College Place, Washington (1982)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Black
University of British Columbia
Vancouver, British Columbia
(1985)

Charles R. Hatch
University of Idaho
Moscow, Idaho (1983)

Janet E. Hohn
U.S. Fish and Wildlife Service
Portland, Oregon (1983)

Denis P. Lavender
Oregon State University
Corvallis, Oregon (1984)

Roger del Moral
University of Washington
Seattle, Washington (1983)

Don Minore
U.S. Forest Service
Corvallis, Oregon (1984)

Richard J. Naskali
University of Idaho
Moscow, Idaho (1984)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

Ronald H. Sauer
Battelle Northwest Laboratories
Richland, Washington (1984)

Steven R. Seavy
Lewis and Clark College
Portland, Oregon (1985)

Kareen Sturgeon
Linfield College
McMinnville, Oregon (1985)

J. Mary Taylor
2718 SW Old Orchard Road
Portland, Oregon 97201
(1983)

Robert Zasoski
University of Washington
Seattle, Washington (1984)

Donald B. Zobel
Oregon State University
Corvallis, Oregon (1983)

*Term of office expires in the year given in parentheses

PUBLISHED QUARTERLY BY WASHINGTON STATE UNIVERSITY PRESS
WITH COLLABORATION OF NORTHWEST SCIENTIFIC ASSOCIATION

Dennis R. Davenport

and

John L. Weaver

Bridger-Teton National Forest
Box 1888
Jackson, Wyoming 83001

Wintering Bald Eagles in Jackson Hole, Wyoming

Abstract

During the extremely cold winter of 1978-79, distribution of approximately 29-32 bald eagles (*Haliaeetus leucocephalus*) coincided with distribution but not abundance of wintering ungulates (available carrion) in Jackson Hole, Wyoming. Subadults comprised 17-19 percent of the population.

Introduction

Herein we report on the first systematic survey of Bald Eagles wintering in Jackson Hole, Wyoming, and comment on the role of ungulate carrion during an extremely rigorous winter.

Methods

Aerial observations were made from a Cessna 180 on 19 January 1979 along major watercourses; ground observations from a vehicle were obtained on 10 days, 14-27 January, from roads adjacent to the same watercourses.

Description of Study Area

Surveys were conducted along approximately 125 km of the Snake River, 25 km of the Gros Ventre River, and 25 km of the Hoback River, in Jackson Hole, northwest Wyoming (Fig. 1). Love and Reed (1968), Shaw (1975), Weaver (1977), and Kiefling (1978) have described the area. Dominant vegetation along the rivers includes narrowleaf cottonwood (*Populus angustifolia* James), blue spruce (*Picea pungens* Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and various willows (*Salix* spp.).

The winter of 1978-1979 brought very cold temperatures to Jackson Hole for sustained periods. During early January, temperatures plummeted to –45°C in some places. Low temperatures for January 1979 averaged 10°C below the average low temperature for that month (–16.3°C, 1959-1978).

Results and Discussion

During January 1979, approximately 29-32 Bald Eagles inhabited Jackson Hole. Aggregations of five to eight eagles were found in three locales: (1) National Elk Refuge (NER), (2) Snake River through South Park, and (3) Snake River from Astoria

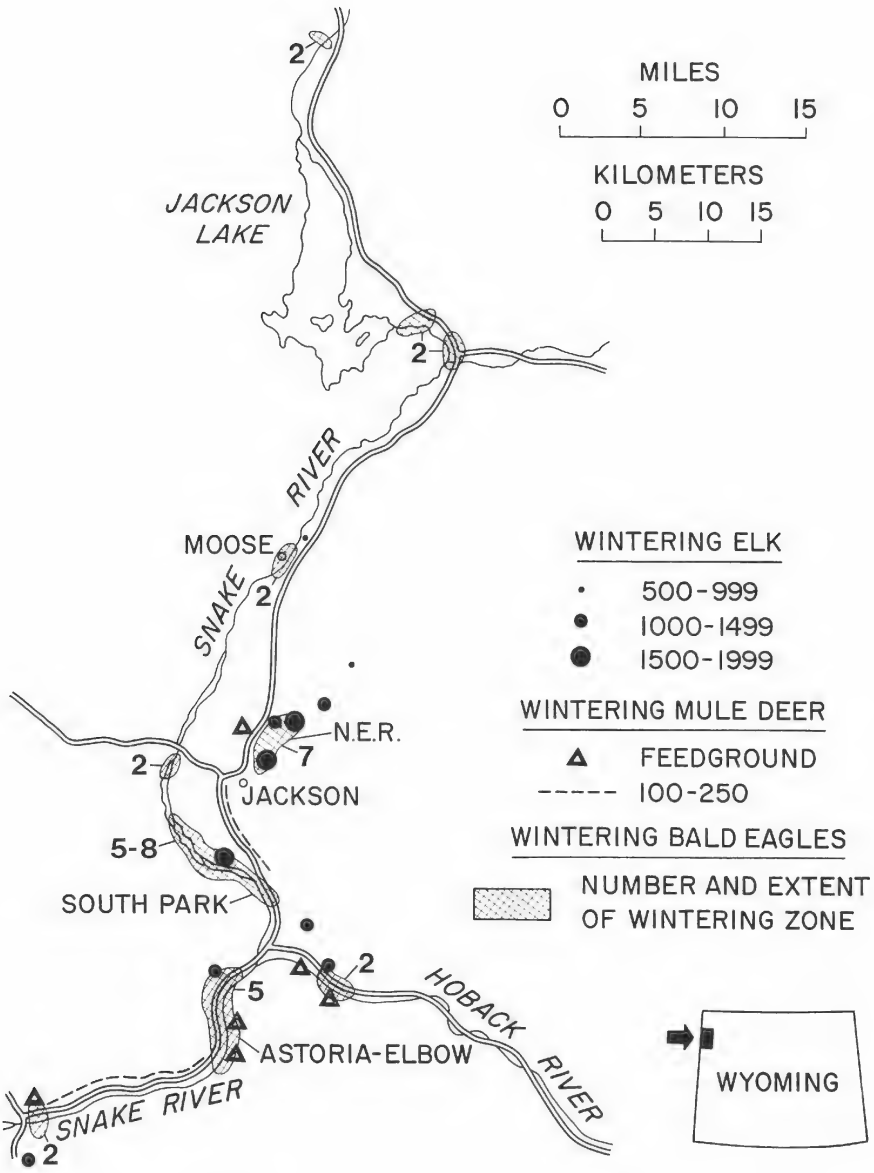


Figure 1. Location of study site.

to the Elbow (Fig. 1). Seven Bald Eagles were observed on the NER during this survey, whereas one to five birds have been reported there in the past five winters.

Five eagles were subadults (17-19 precent). For Yellowstone National Park, Swenson (1975) reported an average (1959-75) mid-winter Bald Eagle population of seven

(range 2-13). Subadults averaged 8 percent but were absent in nine of the 15 winters when eagles were classified (Swenson, 1975). The relatively low percentage of subadult Bald Eagles in northwestern Wyoming during winter may result from a tendency of subadults to winter farther south than adults (Southern, 1963, 1964; Sprunt and Ligas, 1966; Swenson, 1975).

Bald Eagles in Jackson Hole during this period were dispersed in clumps which coincided with the distribution of wintering elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*), mainly at or near State and Federal feedgrounds (Fig. 1). Approximately 78 percent of 46 sightings and all groups greater than two eagles occurred within 3.2 km of these sources of ungulate carrion. In all eight instances where Bald Eagles were observed feeding, the food source was elk or mule deer carrion. Swenson (1975) reported that five of six Bald Eagle wintering areas in Yellowstone National Park were associated with wintering ungulates, with each also having some open water.

Data on amount of ungulate carrion available were limited to the NER and Astoria-Elbow areas. On the NER during December 1978-February 1979, 97 dead elk provided approximately 17,620 kg for carrion feeders, including seven Bald Eagles. During the same period between Astoria and Elbow, 44 ungulates—29 mule deer, 12 elk, and 3 moose (*Alces alces*)—succumbed and furnished approximately 4296 kg. Five Bald Eagles occupied this stretch of the Snake River.

Although several biological factors (i.e., Bald Eagle-coyote (*Canis latrans*) competition) could have influenced the lack of correlation between eagle numbers and amount of ungulate carrion, we reserve a full discussion until more data accrue.

Summary and Conclusions

In most winters, some of the waters amidst Bald Eagle wintering areas in Jackson Hole remain open and provide opportunities for eagles to supplement their diet with fish and/or waterfowl. The two pairs of Bald Eagles at Huckleberry Hot Springs (north of Jackson Lake) and below Jackson Lake Dam (Fig. 1) did winter near open water and away from ungulate herds. The cold winter of 1978-79, however, froze a greater portion (up to 95 percent) than usual, including some stretches not closed since 1949. Consequently, fewer of these supplemental food sources were available to Bald Eagles, whose restricted distribution reflected an even greater reliance upon ungulate carrion.

Our observations in Jackson Hole support those compiled by Spencer (1976) that Bald Eagles wintering in northern zones rely substantially upon carrion for food, especially during severe ice-up periods on lakes and rivers.

Acknowledgments

We thank personnel of Wyoming Game and Fish Department, Grand Teton National Park, and the National Elk Refuge for observations and information. J. H. Hoak, Jr., assisted with aerial observations. D. A. Spencer and J. E. Swenson reviewed the manuscript. The U.S. Forest Service (Bridger-Teton National Forest) supported the study.

Literature Cited

Kiefling, J. W. 1978. Studies on the Ecology of the Snake River Cutthroat Trout. Fisheries Technical Bull. No. 3. Wyoming Game and Fish Department, Cheyenne.

Love, J. D., and J. C. Reed. 1968. Creation of the Teton Landscape. The geologic story of Grand Teton National Park. Grand Teton Nat. Hist. Assn.
Shaw, R. J. 1975. Field Guide to Vascular Plants of Grand Teton National Park and Teton County. Utah State Univ. Press, Logan.
Southern, W. E. 1963. Winter populations, behavior, and seasonal dispersal of Bald Eagles in northwestern Illinois. Wilson Bull. 75:42-55.
———. 1964. Additional observations on winter Bald Eagle populations: including remarks on biotelemetry techniques and immature plumages. Wilson Bull. 76:121-137.
Spencer, D. A. (ed.). 1976. Wintering of the Migrant Bald Eagle in the Lower 48 States. Nat. Agric. Chem. Assoc. Publ. Washington, D.C.
Sprunt, A., IV and F. J. Ligas. 1966. Audubon bald eagle studies 1960-1966. Proc. Nat. Audubon Soc. Convention 62:25-30.
Swensen, J. E. 1975. Ecology of the Bald Eagle and Osprey in Yellowstone National Park. Montana State Univ., Bozeman. M.S. thesis.
Weaver, J. L. 1977. Coyote-food Base Relationships in Jackson Hole, Wyoming. Utah State Univ., Logan. M.S. thesis.

Received April 4, 1980
Accepted for publication January 14, 1981

Daniel J. Vogt

and

Robert L. Edmonds

College of Forest Resources
University of Washington
Seattle, Washington 98195

Nitrate and Ammonium Levels in Relation to Site Quality in Douglas-fir Soil and Litter

Abstract

Nitrate and ammonium levels in the L horizon and soil to a 5 cm depth were analyzed during the months of July and January in three different aged Douglas-fir (*Pseudotsuga menziessi* (Mirb.) Franco) Site Class II stands and four Site Class IV stands in western Washington. Litter and soil ammonium levels in the high site quality (II) stand were significantly different from those in the low site quality (IV) stands. In contrast, however, nitrate concentrations were significantly greater in the high site quality stands. Total N or C did not appear related to the net nirate differences observed between the high and low site quality stands.

Introduction

Douglas-fir response to nitrogen fertilization has been shown to be greater in low site quality stands than in high site quality stands (Gessel and Atkinson ,1979). The response is attributed to differences in levels of available soil N (ammonium and nitrate). Few studies, however, have been conducted to determine in situ levels in soils in the Douglas-fir region. Even fewer studies have reported inorganic N levels in the litter where much of the nutrient release through decomposition is occurring.

Johnson (1979) has examined seasonal changes of available soil nitrogen in low site quality Douglas-fir stands and found ammonium and nitrate concentrations to be low. In a laboratory study of incubated, nonfertilized Douglas-fir soils, Heilman (1974) also found nitrate production to be low (< 3 ppm). Highest levels, however, were from the more productive sites (Heilman, 1974). Vitousek *et al.* (1979) also detected greater nitrate losses from their higher site quality Douglas-fir stands. From these studies, there is the implication that nitrate levels may be related to the site quality of a forest stand. Thus, the estimation of nitrate production (and potential nitrogen loss) in a forested area containing different site classes may be misleading if derived from data obtained from small research plots of only one site class. With many forests mapped as to site class, the possible high correlation of site quality to nitrate levels could prove useful in more accurate estimations of nitrate levels in forested regions.

It was the intent of this study to determine if there are significant differences in ammonium and nitrate levels in litter and soil between high and low site quality closed-canopy Douglas-fir stands.

Methods and Materials

Plots (0.045 ha in area) were established in each of three site class II (high site quality,

King, 1966) and four site class IV (low site quality) Douglas-fir stands. Site class II stands were aged 45, 75, and 175 years, and site class IV stands were aged 45, 75, 120, and 175 years. Six of the stands were located approximately 120 km south of Seattle, Washington, at the Charles Lathrop Pack Experimental Forest of the University of Washington. The site class II, 45-year-old stand was located on nearby Weyerhaeuser property.

The predominant tree species on all plots was Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Understory vegetation consisted of swordfern (*Polystichum munitum* (Kaulf.) Presl.), vine maple (*Acer circinatum* Pursch), Oregon grape (*Berberis nervosa* Pursh), and salal (*Gaultheria shallon* Pursh). In the site class II stands, swordfern was the dominant understory vegetation, whereas salal dominated in the site class IV stands.

Soils in the high site stands were of the Wilkeson Series (fine-loamy, mixed, Eutric Glossoboralfs). Litter ($O_1 + O_2$ horizon) depths in these stands averaged 2.2 ± 1.2 cm. Low site quality soils were fine-loamy mixed, mesic Typic Xerumbrepts of the Baumgard Series with litter depths averaging 3.4 ± 1.5 cm. Both soil types were deep, well-drained, residuum derived from Andesite with the litter classified as duff-mull according to Hoover and Lunt (1952). The climate at Pack Forest is moderate with a rainfall of approximately 100 cm/yr with a winter maximum and a dry summer. Mean annual air temperature is 9.6°C. The elevation of the stands ranged between 340 and 580 m.

Four litter and four soil (0-5 cm depth) samples were collected from randomly located points in each of the seven plots during July 1976 and January 1977. The four soil samples were obtained directly below the four litter samples. Samples were immediately transported to the laboratory and stored at –10°C until analyzed. All samples were randomly withdrawn from the freezer until they were all analyzed.

Using a dial thermometer (Taylor), litter and soil temperatures were recorded in each plot during each sampling period. Soil and litter moisture contents were determined gravimetrically (105°C and 75°C, respectively) on a wet weight basis. The glass electrode method (Peech, 1965) was used to determine pH with ratios of litter and soil to water of 1:10 (w/v) and 1:2 (w/v), respectively.

Litter and sieved soil (< 2 mm) samples were extracted with 2N KCl at 1:5 and 1:25 (w/v) litter and soil solution ratios, respectively. The samples were then shaken for three hours, filtered through GF/A filters, and analyzed for NH_4^+–N and $NO_3^- + NO_2$–N on a Technicon Auto Analyzer II. Hereafter, $NO_3^- + NO_2$–N will be referred to only as NO_3^-–N. This notation assumes that NO_2–N levels were minor compared to the NO_3^-–N levels.

Total nitrogen was determined only from the July samples. Soils were passed through a 2 mm sieve while the litter was ground and passed through a 40 mesh sieve. The samples were then digested using a wet oxidation technique (Parkinson and Allen, 1975) and analyzed on the Tecnicon Auto Analyzer II for NH_4^+–N as a technique for total nitrogen determination. Soil and litter bulk densities were determined in order to calculate nitrogen content (kg/ha). Total carbon was determined on the July samples using a Leco Carbon Analyzer. This includes charcoal carbon as well as the more available carbon.

Results

Temperature, Moisture, and pH

Generally, litter and soil (to a 5 cm depth) temperatures at the time of sampling were not significantly different at the 95 percent level. As expected, the temperatures were warmer in July (litter and soil means ranging from 12.8 to 14.4°C) than in January (5.3 to 8.9°C). No significant temperature differences were observed between site class II and IV except in January in the soil, where the site II stands averaged 8.1°C and site IV stands 5.3°C.

Litter and soil moisture contents (percent by wet weight) were always significantly different, ranging from 54.9 to 71.1 percent in the litter and 25.1 to 35.2 percent in the soil. However, the expected moisture differences between the normally drier July and the more moist January occurred only in the site class II litter (54.9 and 71.1 percent, respectively). Although the site class II soil was more moist in January (35.2 percent in January vs 27.9 percent in July), the difference was not significant. Significantly higher levels between January and July samples did not occur because the week preceding the July sampling period had higher than normal rainfall. Only during January in the soil was there a significant moisture content difference between the site class II (35.2 percent) and site class IV (25.1 percent) stands.

The pH values, ranging from 5.3 to 6.3, usually did not significantly change from July to January or show significant differences between litter and soil, or between site class II and IV stands (Table 1). There was one exception in the soil of the site class II stands during July. The mean pH of 6.3 was statistically different from the litter above it (5.9), the January soil pH level (5.9), and site class IV pH mean in the soil during July (5.3).

TABLE 1. Litter and soil total N and C, NH_4^+-N, NO_3^--N, C/N ratio, and pH in site II and IV Douglas-fir stands in July 1976 and January 1977. Numbers in parentheses are standard errors. Statistical differences were determined using one-way analysis of variance.

	Sampling Period	LITTER Site Class II	LITTER Site Class IV	SOIL (0-5 cm) Site Class II	SOIL (0-5 cm) Site Class IV
NH_4^+-N (ppm)	July	72.1 (11.2)[bc]	110.4 (23.2)[bc]	21.8 (2.4)[b]	14.0 (3.8)[b]
	January	34.7 (6.1)[c]	44.1 (5.7)[c]	3.7 (0.3)	3.2 (0.4)
NO_3^--N (ppm)	July	4.1 (1.5)	1.0 (0.2)[b]	3.1 (1.0)[ab]	1.0 (0.3)[b]
	January	4.5 (2.2)[ac]	0.5 (0.1)[c]	12.2 (2.9)[a]	0.2 (0.02)
Total N (%)	July	1.06 (0.04)[ac]	1.21 (0.05)[c]	0.3 (0.04)	0.23 (0.02)
Total N (kg/ha)	July	398 (92)[c]	476 (67)	975 (161)	654 (130)
Total C (%)	July	43.1 (0.9)[c]	44.3 (0.4)[c]	6.4 (0.8)	6.0 (0.6)
C/N[d]	July	41.2 (1.8)[c]	37.4 (1.4)[c]	21.7 (1.1)	25.8 (1.5)
pH	July	5.9 (0.1)[c]	5.5 (0.3)	6.3 (0.1)[ab]	5.3 (0.3)
	January	5.8 (0.1)	5.9 (0.2)	5.9 (0.1)	5.5 (0.2)

[a]Significant differences at 95 percent level existed between site classes II and IV within a similar substrate and sampling period.

[b]Significant differences at 95 percent level existed between July and January within a similar site class and substrate.

[c]Significant differences at 95 percent level existed between litter and soil within a similar site class and sampling period.

[d]C/N calculated for each sample then $x \pm$ S.E. calculated, rather than the total C mean divided by the total N mean.

Available N in Relation to Site Quality

Litter NH_4^+–N concentrations appeared higher in the site class IV (low site quality) stands than the site class II (high site quality) stands in both July and January (Table 1). The reverse situation occurred in the soil. However, these differences between site classes were not statistically significant in either the litter or in the soil. Ammonium levels in both litter and soil in both site qualities significantly decreased from July to January (Table 1). Extractable NH_4^+–N concentrations were greater in the litter than in the soil in all cases (Table 1).

Generally, NO_3^-–N concentrations were significantly higher in site II than site IV stands ($p < .05$), except for the litter in July (Table 1). There was also a significant decrease in NO_3^-–N from July to January in site IV litter and soil. However, in site II stands, NO_3^-–N levels remained the same in litter but increased significantly in the soil from July to January. A consistent pattern, however, was not observed for NO_3^-–N concentrations. In January, site IV stands showed significantly greater NO_3^-–N concentrations in the litter (0.5 ppm) than in the soil (0.2 ppm), but this situation was reversed in the site II stands (4.5 vs 12.2 ppm, respectively). In July there were no significant NO_3^-–N differences between the litter and soil in either site class.

Total Carbon and Nitrogen and C/N Ratios and Relationships to Available N

The total nitrogen concentration (percent) was three to five times greater in the litter than in the soil (Table 1). Total N concentraion of site IV litter (1.21 percent) was significantly higher than the litter in site II (1.06 percent). However, the reverse was true of the soil N, site II (0.30 percent) vs site IV (0.23 percent) (Table 1). Total N content was not significantly different between litter (476 kg/ha) and soil (to a 5 cm depth) (654 kg/ha) in the site IV stands, but there was a significant difference between the litter (398 kg/ha) and soil (to a 5 cm depth) (975 kg/ha) in the site II stands. No significant differences in total N content appeared between the site IV (654 kg/ha) and site II (975 kg/ha) stands.

Percent carbon was also greater in the litter than in the soil by about seven times (Table 1). There were no significant differences in carbon between site II and IV in either the litter (43.1 percent and 44.3 percent, respectively) or the soil (6.4 percent and 6.0 percent, respectively).

The C/N ratio was greater in the litter than in the soil (Table 1). In both the litter and soil, the mean C/N ratio was similar between site II (41.2 and 21.7, respectively) and IV (37.4 and 25.8, respectively). Relationships between total N and C/N ratios and available N were generally consistent. In the litter, higher total N values and lower C/N ratios were related to high NH_4^+–N but lower NO_3^-–N levels. The situation was slightly different in the soil where the NO_3^-–N values were higher with associated high total N, lower C/N, and high NH_4^+–N levels. Higher C values in the litter and soil also were related to higher total and available N.

Discussion

Site II Douglas-fir stands in western Washington have been shown to produce more wood volume than site IV stands (RFNRP, 1980). This difference is generally attributed to better moisture conditions and higher soil N levels. Inorganic NH_4^+–N constitutes,

in general, less than 1 percent of the total soil N present, and NO_3^-–N an even lower percentage; however, these inorganic nitrogen species are the most important forms in which nitrogen becomes available to trees. Levels of NH_4^+–N and NO_3^-–N, however, are not constant in soils and fluctuate seasonally. For example, Ellis (1974) found that a spring increase in NH_4^+–N levels was followed by a mid-summer decline, an autumn peak, and finally a winter low in maple woodlot and an old field in Ontario. In low site quality Douglas-fir stands in Washington, Johnson (1979) found that mean NH_4^+–N concentrations ranged from approximately 1 ppm in March to a high of 5 ppm in October. Mean NH_4^+–N values obtained in this study for low site quality soils were slightly higher, ranging from 3.2 ppm in January to 14.0 ppm in July. However, the sampling depths in this study were 5 cm, whereas Johnson sampled to 15 cm. Assuming that microbial activity decreases with depth, a dilution effect could account for the lower concentrations observed by Johnson.

In this study there were no significant differences in NH_4^+–N concentrations between site II and Site IV stands in either litter or soil, although NH_4^+–N levels were consistently higher in the litter in site IV stands and generally higher in the soil in site II stands. Expected significant differences in NH_4^+–N concentrations between the high and low site quality stands were not observed. The higher productivity of the site II stands compared to the site IV stands may be explained by the slightly higher soil NH_4^+–N concentrations and total soil N (kg/ha) in the site II stands.

In contrast to both soil and litter NH_4^+–N concentrations, NO_3^-–N concentrations were significantly higher in site II stands than in site IV stands, except for the litter sampled in July. In the soil, NO_3^-–N concentrations ranged from 3.1 to 12.2 ppm in the site II stands but only from 0.2 to 1.0 ppm in the site IV stands. The slightly higher moisture, pH, and temperatures of the soils in site II stands may have enhanced nitrification. These factors are known to influence nitrification (Alexander, 1978). However, Heilman (1974) found that nitrate production in incubated Douglas-fir soils was unrelated to pH, poorly correlated with C/N ratios, but better related to soil organic C and total nitrogen. In this study, higher soil NH_4^+–N, total N, and carbon and pH were generally related to higher NO_3^-–N levels. These relationships seemed to be reversed in the litter.

Soil NO_3^-–N levels in the low site stands studied by Johnson (1979) did not exceed 0.3 ppm and were similar to those found in this study. Johnson also found no relationship between NH_4^+–N and NO_3^-–N concentrations and found higher soil NO_3^-–N during the winter months. In this study, the January levels of soil NO_3^-–N were greater than in July in the site II stands but not in the site IV stands. The increase in soil NO_3^-–N with increase in site quality found in this study was also observed by Heilman (1974). He found greater NO_3^-–N production in incubated high site Douglas-fir soils (2.8 ppm, site index 125) than in lower site soils (0 to 0.1 ppm, site index 94). These NO_3^-–N values, however, are somewhat lower than those observed in this field study. Vitousek *et al.* (1979) also presented evidence that NO_3^-–N production may be influenced by site quality. A study by Youngberg (1978) showed that litter and soil with highest sustained N mobilization rates come from the highest site quality Douglas-fir types.

The higher concentrations of NH_4^+–N in the litter in comparison to the soil in both site II and site IV stands probably reflects the higher mineralization rates in the

litter. Van Praag and Weissen (1973) also reported that litter had higher NH_4^+–N concentrations than A horizon soil in beech stands in Belgium.

Higher concentrations of litter NH_4^+–N in the site IV than in site II stands may indicate a more active microbial immobilization of NH_4^+–N and/or greater tree uptake in the site II stands. The total N concentration (percent) in the litter of the site IV stands was significantly greater than that in the site II stands; however, the total N content (kg/ha) was not significantly different.

The following conclusions can be drawn from this study:

1. There was no significant difference between NH_4^+–N concentrations in litter and soil in high and low site quality stands. However, litter NH_4^+–N levels were always higher in site IV stands, whereas soil NH_4^+–N levels were always higher in site II stands.
2. Higher NH_4^+–N concentrations were observed in July than in January in both site II and site IV stands in both litter and soil.
3. Generally, significantly higher NO_3^-–N concentrations occurred in site II stands (3.1 to 12.2 ppm) than in site IV stands (0.2 to 1.0 ppm). Levels in high site stands are as high as those reported for eastern deciduous forests.
4. Highest NO_3^-–N concentrations were observed in January in the high site stands, but the reverse situation occurred in the low site stands.
5. There was little apparent relationship between net NH_4^+–N and NO_3^-–N concentrations.
6. Litter NH_4^+–N levels were higher than soil NH_4^+–N levels in all cases, but no consistent pattern existed for NO_3^-–N.
7. Higher levels of NH_4^+–N were related to lower C/N ratios and higher total N in litter and soil when comparing site II and IV stands. Higher values of NO_3^-–N were related to lower C/N ratios and higher total N only in soil when comparing site II and IV stands, whereas the reverse occurred in the litter.
8. Environmental variables (litter and soil moisture, temperature, and pH) were not very different between sites II and IV, although site II soils were slightly warmer, more moist, and had slightly higher pH values. These differences may have favored decomposition and NH_4^+–N and NO_3^-–N production.

Acknowledgments

This research was supported by National Science Foundation Grant No. DEB74-20744 A06 to the Coniferous Forest Biome, Ecosystem Analysis Studies. This is contribution number 380 from the Coniferous Forest Biome. The authors thank Francis Olszewski for the help she gave in analyzing the soil samples.

Literature Cited

Alexander, M. 1977. Introduction to Soil Microbiology. 2nd edition. John Wiley, New York.

Ellis, R. C. 1974. The seasonal pattern of nitrogen and carbon mineralization in forest and pasture soils in southern Ontario. Can. J. Soil Sci. 54:15-28.

Gessel, S. P., and W. A. Atkinson. 1979. Forest fertilization practices. Pp. 293-298 *in* P. E. Heilman, H. W. Anderson, and D. M. Baumgartner (eds.), Forest Soils of the Douglas-fir Region. Cooperative Extension Service, Washington State Univ., Pullman.

Heilman, P. E. 1974. Effect of urea fertilization on nitrification in forest soils in the Pacific Northwest. Soil Sci. Soc. Amer. Proc. 38:664-667.

Hoover, M. D., and A. H. Lunt. 1952. A key for the classification of forest humus types. Soil Sci. Soc. Amer. Proc. 16:368-370.
Johnson, D. W. 1979. Some nitrogen fractions in two forest soils and their changes in response to urea fertilization. Northw. Sci. 53:22-32.
King, J. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser Forestry Paper No. 8. Centralia, Wash.
Parkinson, J. A., and S. E. Allen. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun. Soil Sci. Plant Anal. 6:1-11.
Peech, M. 1965. Hydrogen-ion activity. Pp. 914-926 *in* C. A. Black (ed.), Methods of Soil Analysis. Part 2. Chemical and microbiological properties. Agron. No. 9. Amer. Soc. Agron., Madison, Wis.
Regional Forest Nutrition Research Project (RFNRP) Biennial Report 1978-1980. Institute of Forest Resources Cont. No. 39. College of Forest Resources, Univ. of Washington, Seattle.
Van Praag, H. J., and F. Weissen. 1973. Elementals of a functional definition of oligotroph humus based on the nitrogen nutrition of forest stands. J. Appl. Ecol. 10:569-583.
Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, W. A. Reiners, and R. L. Todd. 1979. Nitrate losses from disturbed ecosystems. Science 204:469-474.
Youngberg, C. T. 1978. Nitrogen mineralization and uptake from Douglas-fir forest floors. Soil Sci. Amer. J. 42:499-502.

Received April 29, 1980
Accepted for publication June 23, 1981

Duncan S. Campbell
and
Daniel J. Johnson
Undergraduate Research Project
Geology Department
University of Puget Sound
Tacoma, Washington 98416

Bouguer Gravity Study of Enumclaw/Pinnacle Peak, Washington

Abstract

A Bouguer gravity survey in the area of Enumclaw and Pinnacle Peak, Washington, which is located at the western edge of the Cascade Range, revealed a positive gravity anomaly associated with Pinnacle Peak and a continuous positive gravity anomaly associated with two lesser peaks. The two lesser peaks were interpreted as surface exposures of an Eocene or post-Eocene dike which was partly covered by Pleistocene deposits. The appendix of this paper presents the computer program used in this study to model the mass attraction of isolated peaks by subdividing the peak into a set of vertical prisms and summing the calculated mass attraction of each prism.

Introduction

Pinnacle Peak rises 350 m (1050 ft) above an otherwise featureless plain in the vicinity of Enumclaw, Washington. This plain is composed of Pleistocene glacial deposits and a recent mudflow (Osceola mudflow; 4700 BP) from Mount Rainier (Crandell, 1963). Because of this cover, except for outcrops on Pinnacle Peak and neighboring peaks, bedrock cannot be observed directly. Near the summit of Pinnacle Peak, outcrops of andesite with well developed columnar jointing are found. It has been hypothesized (Z. F. Danes, pers. comm.) that these peaks were derived as volcanic plug domes.

Many more small isolated peaks similar to those investigated in this survey are found to the north and south of this area. All of these peaks are found in a 5 km wide band along the western margin of the Cascade Range that extends for 20 km from 4 km south of Pinnacle Peak near Page Creek at the southern end to Palmer at the northern end. Vine (1969) has mapped the Cumberland Quadrangle, which includes the northern half of this band, and has described several igneous sills and dikes within this quadrangle. He has tentatively assigned these intrusions to an Oligocene age.

The topographic map (Fig. 1) shows the area covered by this survey. Pinnacle Peak is located at the southwest corner of sec. 31, and two lesser peaks are located in the northwest corner of sec. 36 and the southwest corner of sec. 25, respectively, T. 20N, R. 6E. The two lesser peaks are separated in a north-south orientation by 700 m.

The purpose of this study is to search for gravitational anomalies caused by possible volcanic conduits associated with Pinnacle Peak. Because of the overlying alluvium, we must rely on indirect means of exploration. Gravitational methods are based on the measurement at the earth's surface of small variations in the gravitational field which are caused by lateral variations in the distribution of mass in the earth's crust.

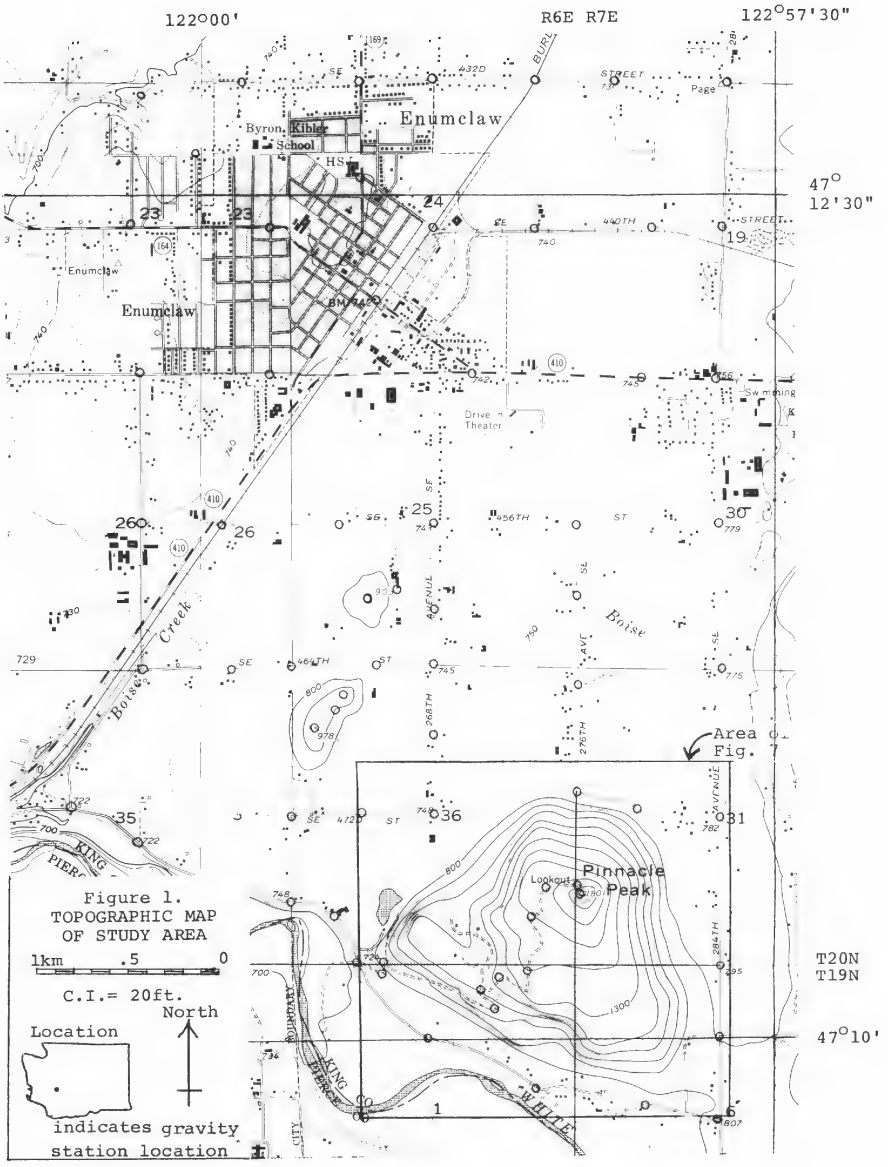


Figure 1. Topographic map of study area.

Data Acquisition and Reduction

Gravity measurements were taken at 71 locations throughout the 20.8 km^2 study area, giving a density of 3.4 stations per km^2. Station elevations were determined with an aneroid barometer with loops tied to road intersections where surface elevations are

known from U.S. Geological Survey topographic maps. Elevations obtained from survey maps are accurate to ± 0.6 m (± 2 ft). Gravity observations have a precision of approximately ± 0.02 mgals. Barometric elevations are accurate to ± 6 m.

The observed gravity values were corrected for the variation of gravity with latitude and elevation as well as the attraction of mass above sea level.

The system used in this study for accounting for the attraction of material above sea level differs from the standard method. Normally, the attraction of the mass below a station and above sea level is approximated by an infinite slab of material. Then, if the topography is irregular, the attraction of all excess mass above the level of the station—as well as mass deficiencies from voids below the level of the station—is taken into account in a process of "sculpting." This is the "terrain correction."

In this study, conversely, the unique topographic setting of this area—characterized by isolated hills surrounded by flat plains—allowed for direct "building" of the terrain above sea level. The attraction of the material below the level of the plain for stations not near the peaks (below an elevation of 283 m (750 ft) for stations on Pinnacle Peak, and below 280 m (740 ft) for stations on the two lesser peaks) was approximated by an infinite plate with an assumed density of 2.67 gm/cm^3. For stations on and near the peaks, a computer was used to model (by the method of prisms (see appendix and Danes, 1960)) the gravitational attraction of the material of the peaks above the level of the infinite plate. For this determination, a density of 2.52 gm/cm^3 was used. This density value was found in a laboratory analysis of rock samples. (This density could be too low and would perhaps be greater if fresher samples were obtained.) The calculated mass attraction of the peaks was added to the attraction of the infinite plate below to achieve the total mass attraction.

Results

The resulting Bouger gravity anomaly map of the Enumclaw/Pinnacle Peak area is shown in Figure 2. Residual gravity was derived from the Bouguer gravity by subtracting the regional anomaly derived from Danes' data (to be published). The resulting gravity map is shown in Figure 3.

The residual gravity values show slight variations over the area ranging from +3 mgals to −1.5 mgals. Positive gravity anomalies are correlated with Pinnacle Peak and the two lesser peaks.

Interpretation

The magnitude of the Pinnacle Peak anomaly proved to be much less than anticipated. In addition, the location of the center of this anomaly with respect to the peak is difficult to define.

Attention was diverted from the Pinnacle Peak anomaly because of the above-mentioned problems and also because a full profile could not be constructed across the peak since the area to the east and south is not accessible by road.

Instead, the anomaly associated with the two lesser peaks was chosen for analysis in this report. This oval shaped anomaly is 1.5 mgals in magnitude and encloses both peaks. The authors attribute this anomaly to a north-south oriented dike which is exposed at the surface in the form of the two peaks. To demonstrate this possibility, we will model the dike—in the first approximation—as a horizontal cylinder. This

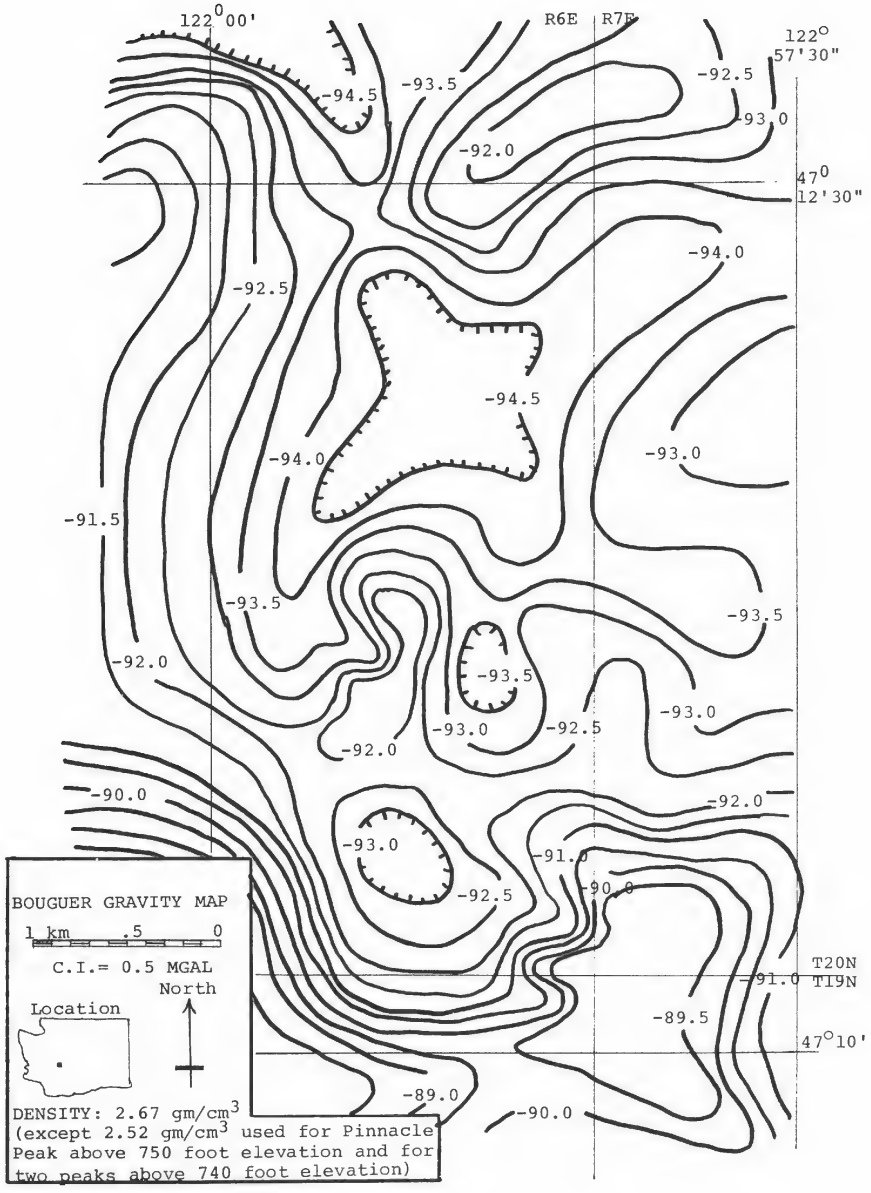


Figure 2. Bouguer gravity map of study area.

formation may not be geologically realistic but should be sufficiently so to determine if the postulate is reasonable.

Figure 4 shows two profiles across the anomaly associated with the two peaks. The

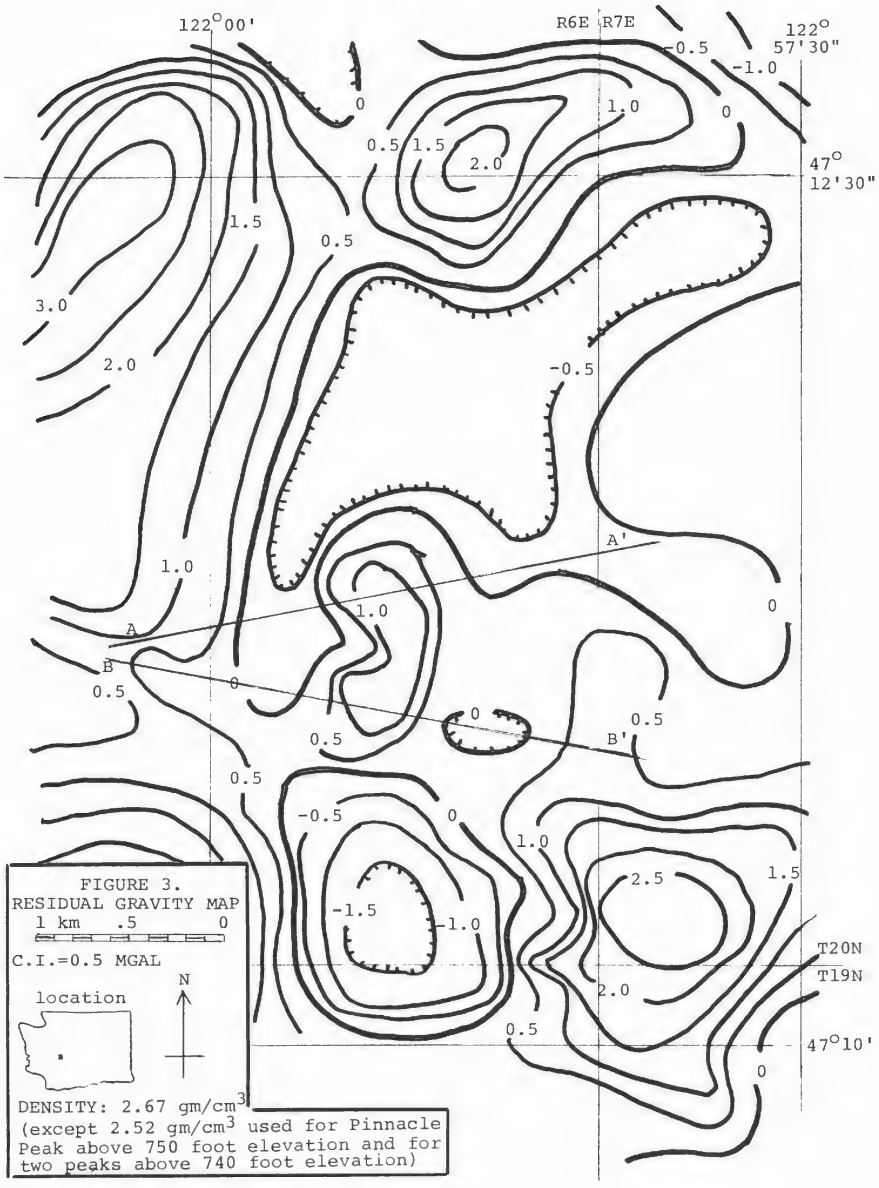


Figure 3. Residual gravity map of study area.

gravitational effect of neighboring masses was estimated and subtracted from these profiles. In this way, the anomaly was isolated and its magnitude was found to be 2.0 mgals.

The half width of an anomaly, $X_{½}$, is defined as the distance from the center of the

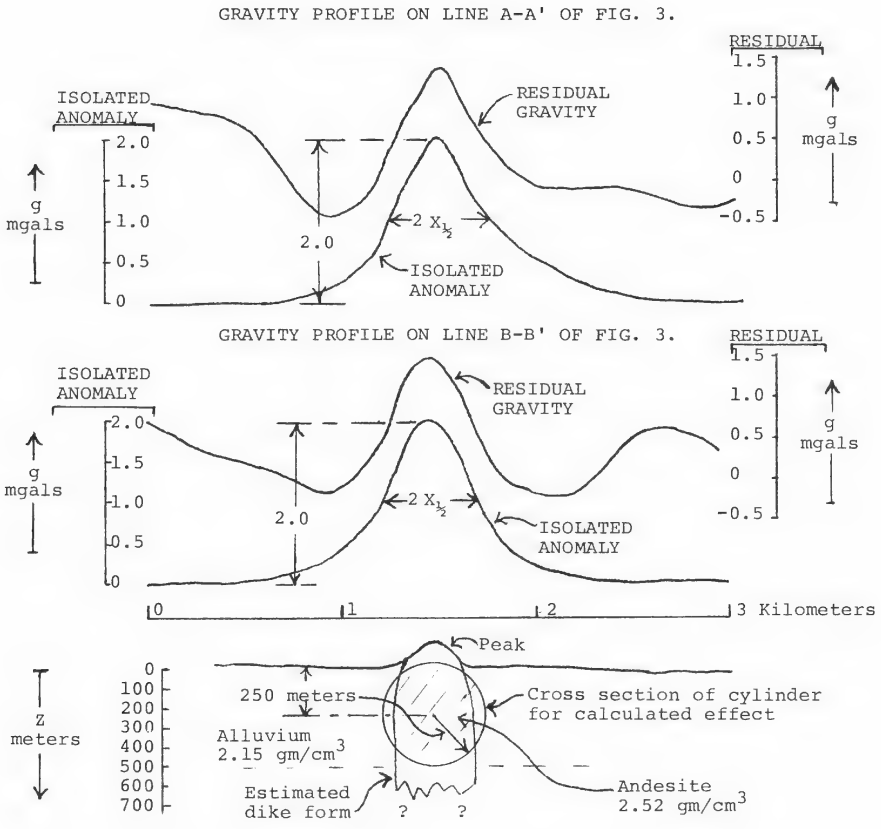


Figure 4. Gravity profiles and interpretation.

anomaly to the point at which the gravity value has fallen off to half of its maximum value, which is equal to the depth to the axis of a horizontal cylinder (Dobrin, 1976; p. 468). In this case, the half width of the anomaly, and thus the depth, is equal to 250 m.

The radius of the cylinder in kilometers is given by Dobrin to be

$$R = \sqrt{\frac{g^2_{max}\ Z}{41.93}} \qquad \text{(eq. 1)}$$

where g_{max} is the maximum gravity value of the profile in mgals, Z is the depth in kilometers, and ρ is the density contrast in gms/cm^3. We know, however, that this object is exposed at the surface in the form of the two peaks. Thus, we can assume the radius to be equal to the depth, and we solve for the density contrast by using equation 1, which can be written as

$$\rho = \frac{g^2_{max}\ Z}{41.93\ R^2} \qquad \text{(eq. 2)}$$

In this case, with R and Z equal to 250 m, and g_{max} equal to 2.0 mgals (from Fig. 4), we find that the calculated density contrast is 0.38 gm/cm^3. This calculated density contrast seems reasonable. Based on an assumed density of 2.15 gm/cm^3 for the saturated glacial sediments and 2.52 gm/cm^3 for the andesite of the peaks, we would expect a density contrast of 0.37 gm/cm^3. The agreement between the theoretical model and geological constraints supports the interpretation that these peaks are the surface exposure of a dike.

The geology of this area has not been mapped, so geological information from surrounding areas must be used in order to determine the age of this dike. At a location 7 km to the northwest of the two peaks in sec. 10, T. 20N, R. 6E., a well (McCullock-Krainick #1) was drilled through 453 m (1370 ft) of Pleistocene glacial drift. Below this was found 1297 m (3891 ft) of Eocene sands and shale. Of course, in the area of the two peaks, which is only 1.5 km from the western edge of the Cascade Range, one would expect substantially less Pleistocene fill. With the above information, the authors suspect that these peaks were formed as a result of Eocene or post-Eocene intrusions and were partly covered later by Pleistocene deposits.

The results of this geophysical survey are interesting and deserve further attention. The geology of this region should be mapped, and work should be done to determine its geological history.

A magnetic survey of this area could be of value and might lead to the discovery of similar intrusions which do not crop out. It should be mentioned, however, that a ground based survey would be difficult to carry out due to interference from numerous power lines, fences, railroad tracks, etc., in the area.

Appendix: Computer Program to Model Gravity Field of Isolated Peaks by Method of Prisms

Introduction

This program makes it possible to compute the vertical component of the gravitational attraction of a mass at the center of each grid section of a partitioned area. The system used is similar to that of Danes (1960). By plotting calculated gravitational attraction values on a map and contouring, the gravitational attraction at any given point on the map may be read directly. This method is well suited for isolated hills where the gravitational effects of the nearly flat surrounding topography may be ignored and also for high density surveys where many terrain correction values must be calculated in the same area.

Data Preparation

To use this program, the terrain must be digitized. This procedure is done by subdividing a rectangular topographic map of the area to be digitized into a uniform grid. This program can accommodate up to 50 sections on a side. The numbers of grid divisions in the east-west and north-south directions are recorded. These are labeled "IDIMEA" and "IDIMSO," respectively, in the program. The elevation in ft above the chosen reference level of each grid area is then averaged. The spacing between each grid is measured, converted to centimeters, and recorded. This is labeled "WIDTH" in the program. A data file is constructed for the recording of the elevation values obtained above. In the program this data file is labeled "DIGIT.DAT." Values are listed consecutively in the data file in integer format. The output of this program is a sequential listing of the gravitational attraction of the feature at the centerpoint of each of the same grid divisions used for the input.

Theory

The vertical component of mass attraction of a hill at a point on the surface is calculated by summing the contributions of many subdivisions of that hill. Each subdivision is prismatic in shape with a width equal to the grid spacing and a height equal to the average elevation of the top of the prism minus the elevation of an arbitrary reference level. In most applications, this reference level will be the lowest point of the hill.

The vertical component of mass attraction of each prism can be derived in the following manner:

1. The prism is mathematically subdivided into smaller subdivisions. The gravitational effect of each section is approximated by assuming that its entire mass is concentrated at a point at its

center. We are interested in the vertical component dg of this increment at a point P. This is given by the equation

$$dg = Gdm \frac{Z}{r^3} \qquad \text{(eq. 3)}$$

where G is the gravitational constant and dm is the mass element. Figure 5 shows the relation between the mass element and the point P in terms of lengths Z in the vertical component and r in the radial.

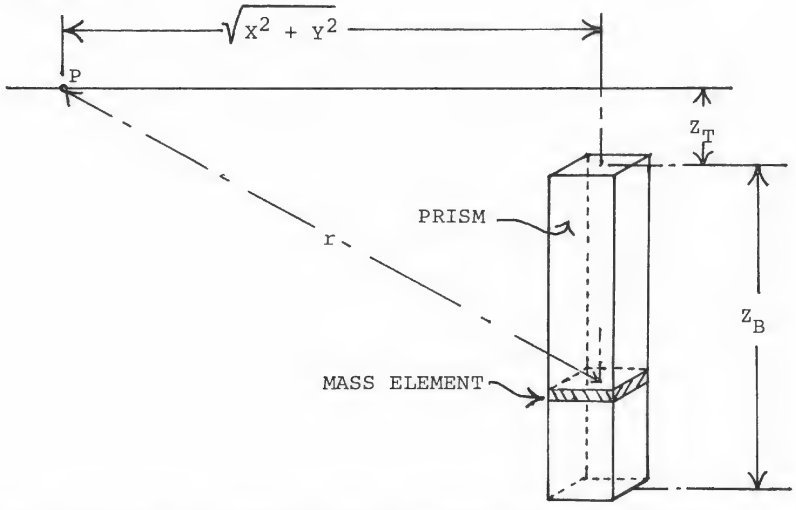


Figure 5. Quantities used in deriving formula for gravitational attraction of a prism.

2. The radius can be expressed in three dimensions by subtracting the equation

$$r = \sqrt{X^2 + Y^2 + Z^2} \qquad \text{(eq. 4)}$$

where X and Y are horizontal components in north-south and east-west orientations, respectively.

3. The mass element may be replaced by the quantity ρdV (eq. 5)
where ρ is the density and V is the volume element.

4. The volume element is given by

$$dV = w^2 dZ \qquad \text{(eq. 6)}$$

where w is the width of the prism in the X or Y direction.

5. We now find that the magnitude of attraction of each section of the prism is given by the equation

$$dg = G\rho w^2 \frac{ZdZ}{(X^2 + Y^2 + Z^2)^{3/2}} \qquad \text{(eq. 7)}$$

6. The vertical component of attraction of the prism can be obtained by integrating over the length of the prism.

$$g_{prism} = G\rho w^2 \int_{Z_T}^{Z_B} \frac{ZdZ}{(X^2 + Y^2 + Z^2)^{3/2}} = G\rho w^2 (X^2 + Y^2 + Z^2)^{-1/2} \Big]_{Z_B}^{Z_T} \qquad \text{(eq. 8)}$$

where Z_T and Z_B are the dimensions of the top and bottom of the prism, respectively.

7. This equation can be reduced to the form

$$g_{prism} = G\rho w \left[\frac{1}{\sqrt{m^2 + n^2 + (Z_T/w)^2}} - \frac{1}{\sqrt{m^2 + n^2 + (Z_B/w)^2}} \right] \qquad \text{(eq. 9)}$$

where m and n are the number of grid units east-west and north-south between the prism and the point P.

If we used the above method for that prism on which the point P lies, the gravity field for this prism would become infinite because we have assumed that the mass of the prism is concentrated along the central axis. For this case, the gravitational attraction is determined by the use of a vertical cylinder with a cross-sectional area equal to that of the prism which it replaces.

1. The appropriate radius is given by
$$R = w/\sqrt{\pi} \qquad \text{(eq. 10)}$$
in order that the horizontal cross-section of the cylinder match that of the prism.
2. The equation for the attraction of this central cylinder is given by
$$g_{\substack{\text{central}\\ \text{prism}}} = 2\pi G\rho\,([S_T - Z_T] - [S_B - Z_B]) \qquad \text{(eq. 11)}$$
where S_T, S_B, and Z_B relate to the dimensions indicated in Figure 6.

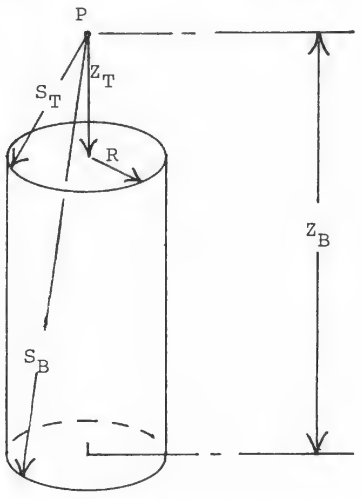


Figure 6. Quantities used in deriving formula for gravitational attraction of the central cylinder.

3. Since, however, point P is in the upper surface of the equivalent cylinder, we have Z_T equal to zero, S_T equal to R and, therefore
$$g_{\substack{\text{central}\\ \text{prism}}} = 2\pi G\rho\,(R - \sqrt{R^2 + Z_B^2}) + Z_B \qquad \text{(eq. 12)}$$
4. Upon substitution of the appropriate value for R given above, this equation becomes
$$g_{\substack{\text{central}\\ \text{prism}}} = 2\pi G\rho \left[\frac{w}{\sqrt{\pi}} + Z_B - \sqrt{\frac{w^2}{\pi} + Z_B^2} \right] \qquad \text{(eq. 13)}$$
and upon factoring, this equation becomes
$$g_{\substack{\text{central}\\ \text{prism}}} = 2\pi G\rho w \left[\frac{1}{\sqrt{\pi}} + \frac{Z_B}{w} - \sqrt{\frac{1}{\pi} + \left(\frac{Z_B}{w}\right)^2} \right] \qquad \text{(eq. 14)}$$

Implementation

Data are prepared as outlined above. The programs are linked and compiled according to the current system commands for FORTRAN-IV. The program will then be executed in the following general steps:

I. Requests
   1. Density of hill.
   2. Width of grid spacing.
   3. Number of grid divisions in east-west direction.
   4. Number of grid divisions in north-south direction.

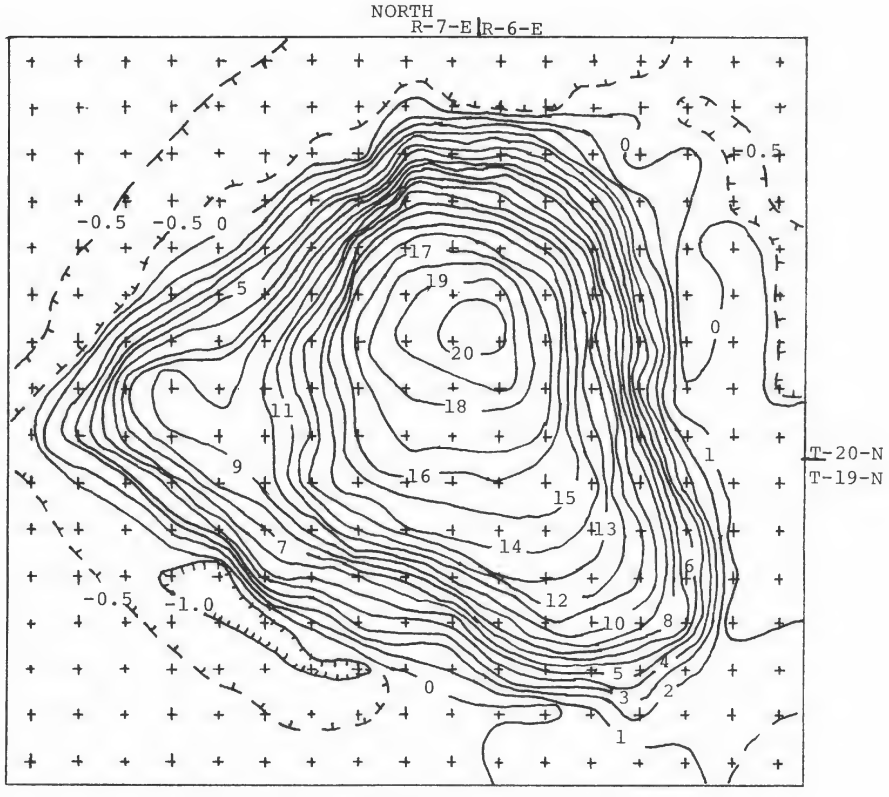
II. Reads the matrix of elevations from the file.

III. Sequentially, for the center point of each grid unit:
   1. Calculates the vertical component of mass attraction of every prism in the matrix except for the central prism using equation 9.
   2. Calculates the vertical component of mass attraction of the central prism using equation 14.
   3. Sums the vertical mass attraction of all prisms and the central prism.
   4. Prints the sum after converting to mgals.

Example

This program was used to obtain terrain corrections for gravity measurements on Pinnacle Peak. Only the mass of Pinnacle Peak above the 750 ft elevation of the surrounding flat plain was modeled. In this case, the density of the peak was assumed to be 2.52 gm/cm^3 as measured for several rock samples taken from the peak. The area of Pinnacle Peak was partitioned into a grid system with dimensions of 17 by 16 grid spaces east and south, respectively. Each grid section had a width of 12,000 centimeters. The area covered by this grid system is indicated in Figure 1.

After running the program, the output was plotted on the same grid system used for the input and the values contoured. The resulting map of the gravity field of Pinnacle Peak is shown in Figure 7. The center point of each grid section has been indicated by a "+" symbol.



+ indicates centerpoint of grid unit

Grid spacing: 1,200 cm. Contour interval: 1 mgal

Area of this map indicated in Figure 1.

Calculations based on attraction of mass above 750 foot elevation and density of 2.52 gm/cm^3.

Figure 7. Gravity field of Pinnacle Peak.

Figure 8. Fortran Program to model gravitational mass attraction of isolated peaks by method of prisms.

```
      DIMENSION MATRIX (50,50)
      OPEN(UNIT=1,NAME='DIGIT.DOT',TYPE='OLD')
      WRITE(7,10)
10    FORMAT(1X,'ENTER DENSITY,GRID WIDTH,DIM. EAST, DIM. SOUTH')
      READ(5,11) DENSE, WIDTH, DIMSO, DIMEA
11    FORMAT(1X,2F,21)
        DO 2,I=1,IDIMSO
        DO 2,J=1,IDIMEA
 2    READ(1,5,END=1) MATRIX(J,I)
 1    DO 37,K=1,IDIMSO
      DO 37,L=1,IDIMEA
 7    SUMG=O.
 5      FORMAT(I)
      SOUTH=FLOAT(K)
      EAST=FLOAT(L)
      HEIGHT=FLOAT(MATRIX(L,K))*30.48
        DO 30,I=1,IDIMSO
        DO 30,J=1,IDIMEA
      A=FLOAT(J)
      B='FLOAT(I)
      ATRIX=MATRIX(J,I)*30.48
17      IF (I.EQ.SOUTH)GO TO 20
        GO TO 25
20        IF (J.EQ.EAST) GO TO 35
25    C=.666667E-7*DENSE*WIDTH
      D1=(ABS(EAST-A))**2.
      D2=(ABS(SOUTH-B))**2.
      D3=(ABS(HEIGHT-ATRIX)/WIDTH)**2.
      E=1./SQRT((ABS(EAST-A))**2.+(ABS(SOUTH-B))**2.+
     1(HEIGHT/WIDTH)**2.)
      PRISM=C*(1./SQRT(D1+D2+D3)-E)
30      SUMG=SUMG + PRISM
      SUMG=SUMG*1000.
        GO TO 37
35      PRISM=.418879*10.**(-6.)*DENSE*WIDTH*(.56419
      1+HEIGHT/WIDTH—SQRT(1./3.14159+(HEIGHT/WIDTH)**2))
        GO TO 30
37    WRITE(7,40) SUMG
40    FORMAT(F7.2)
      REWIND 1
45      END
```


Acknowledgments

Our thanks are expressed to our thesis advisor, Dr. Z. F. Danes, for his help and direction. We wish to thank the University of Puget Sound Geology Department for the use of the gravity meter and the Computer Sciences Department for computer time.

Literature Cited

Crandell, D. R. 1963. Surficial Geology and Geomorphology of the Lake Tapps Quadrangle, Washington. U. W. Geological Survey Prof. Paper 388-A.

Danes, Z. F. 1960. On a successive approximation method for interpreting gravity anomalies. Geophysics 25:1215-1228.

Dobrin, B. 1976. Introduction to Geophysical Prospecting. 2nd ed. McGraw-Hill Book Co., New York.

Vine, J. D. 1969. Geology and Coal Resources of the Cumberland, Hobart, and Maple Valley Quadrangles, King County, Washington: U.S. Geol. Survey Prof. Paper 624.

Received May 20, 1981
Accepted for publication December 4, 1981

J. H. Scurlock

987 Sauk City Road
Concrete, Washington 98237

R. G. Mitchell

Silviculture Laboratory
Pacific Northwest Forest
and Range Experiment Station
U.S. Department of Agriculture
Bend, Oregon 97701

and

K. K. Ching

School of Forestry
Oregon State University
Corvallis, Oregon 97331

Insects and Other Factors Affecting Noble Fir Seed Production at Two Sites in Oregon[1]

Abstract

Twenty cones from eight noble fir (*Abies procera*) were dissected in 1977 (a low cone year) at two sites in Oregon and found to average 773 seeds per cone (range 559 to 964); 63 percent of the seeds were unfilled, 36 percent infested by insects, and 1 percent were sound. Nine species of insects were associated with seed damage. Two species of lonchaeid flies and a seed chalcid were associated with 94 percent of the damage. Slight damage was noted from four species of Lepidoptera. Two midge species were common in cones, but their contribution to damage could not be established. Some of the insects could survive on unfilled seed, suggesting that the number of empty seeds could have been underestimated.

Introduction

Noble fir (*Abies procera* Rehd.) grows extensively at high elevations along the Oregon and Washington Cascade Range and in fragmented populations in the middle portions of the Coast Ranges. In the Cascades, it extends south from Stevens Pass in Washington to the McKenzie River in Oregon. Farther south, it merges with the ecologically and taxonomically similar California red fir (*A. magnifica* A. Murr.) (Franklin,1964). The tree is prized in commerce because of good form and growth rate (Herman *et al.*, 1978) and its preferred status in the Christmas tree market. It is also resistant to the balsam woolly adelgid (*Adelges piceae* (Ratzeburg)), a serious, introduced pest of subalpine fir (*A. lasiocarpa* (Hook.) Nutt.) and Pacific silver fir (*A. amabilis* (Dougl.) Forbes) in the same elevation zone (Mitchell, 1966). These desirable characteristics, coupled with recent, accelerated cutting at high elevations, have dramatically increased the demand for noble fir seed. This demand has focused attention

[1]This work is based on a dissertation submitted in 1979 by the senior author in partial fulfillment of an MS degree, School of Forestry, Oregon State University, Corvallis 97331.

on how little is known about the reproductive biology of noble fir and factors affecting it.

This paper documents a study of noble fir seed production in 1977 at two places in Oregon. Objectives were to estimate seed potential and to identify the factors preventing achievement of full potential. Insect damage, its distribution and appearance, was emphasized because this is one factor affecting seed survival that can be regulated.

Methods and Procedures

Most of the investigation was conducted in the Cascade Range, at a site about 30 km east of Molalla, Oregon. Elevation of the study site was 1100 m, and the stand in the area was dominated by 40-year-old noble fir, 6-20 m tall. Another site for corroborative biological observations was established in the Coast Range at 1100 m, near the top of Mary's Peak. This site was about 15 km west of Corvallis, and the stand there was essentially pure, old-growth noble fir, 10-30 m tall.

For regular study, 18 trees with two or more cones per tree were selected at the Cascade site, five trees with five or more cones per tree at Mary's Peak. The study trees were widely dispersed at both localities because 1977 was a poor cone year throughout the region, and candidate trees were hard to find. Beginning 9 June, trees at both sites were climbed every five to seven days. Cone and insect development were observed, and cones were collected for dissection and rearing in the laboratory. Additionally, four to seven cones were bagged weekly (nylon laundry bags with 90 holes/cm^2) at the Cascade site to determine attack periods for insects pests. Insects reared from the collections were identified by specialists at the Systematic Entomology Laboratory, ARS, Beltsville, Maryland.

Another sample of 20 cones from eight randomly selected trees (collected 29 August) at the Cascade site was used to determine (1) seed potential, (2) number of seeds per cone site, (3) variance in cone size, (4) distribution of insects within cones, and (5) effects of insects and unfilled seed on seed production. Six of the sample trees had three cones per tree; two trees had one cone each. All cones came from the top whorl of the trees.

Collected cones were weighed (fresh weight), measured for length, and cut into thirds. Every seed was examined and classified as apparently undamaged or damaged by cone moths or cone maggots. Seeds that appeared undamaged were X-rayed according to standard procedures (Simak, 1970) to determine the number filled, unfilled, or infested with chalcid wasps. Seeds infested with chalcids were subsequently placed in rearing to determine the wasp's emergence pattern and the number that would remain in the seed for extended diapause.

A nested analysis of variance was used to compare the relative contributions of within- and among- tree variation—the response variables per cone being number of seeds, length, and weight. Numbers of insects in cone thirds were compared by one-way analysis of variance. Relationships between the dependent variables (length and weight of cones) were investigated by a linear regression analysis. The established level of statistical significance for all tests was $P < 0.01$.

Results

The number of seeds per cone averaged 733 (SD = 103) and ranged from 559 to 964.

The mean weight for green, mature cones was 314 g (SD = 79 g); mean length was 15.8 cm (SD = 1.7 cm). The between-tree variation of weight and length was significantly greater than within-tree variation. A weighted (number of cones per tree) regression ($Y = 454.7 + .90X$) to predict mean seed production per cone per tree from the mean weight of the collected cones proved significant and accounted for 62 percent of the variation in number of seeds per cone. The additional contribution of cone length to this relationship was not significant.

Only 0.7 percent of the 14,650 seeds examined proved sound, 63.3 percent were unfilled and presumably unpollinated, and 36 percent were damaged by insects. The nine species of insects found to be related to seed damage were:

1. *Megastigmus pinus* Parfitt (Hymenoptera:Torymidae)
2. *Earomyia barbara* McAlpine (Diptera:Lonchaeidae)
3. *E. longistylata* McAlpine (Diptera:Lonchaeidae)
4. *Eucosma* sp. (prob. *siskiyouana* (Kearfott)) (Lepidoptera:Olethreutidae)
5. *Laspeyresia* sp. (prob. *bracteatana* (Fernald)) (Lepidoptera:Olethreutidae)
6. *Dioryctria* sp. (prob. *abietivorella* (Grote)) (Lepidoptera:Pyralidae)
7. Unknown looper (prob. in genus *Eupithecia*) (Lepidoptera:Geometridae)
8. *Dasineura* sp. (Diptera:Cecidomyiidae)
9. Unknown resin midge (prob. genus *Resseliella*) (Diptera:Cecidomyiidae)

The first three species were associated with about 94 percent of the insect damage. The impact of gall midges (family Cecidomyiidae) was confounded by associated insects and not evaluated, although 100 percent of the cones and 7 percent of the seed were associated with this species. Cone moths (Lepidoptera) did not prove important in the total impact, but some samples showed damage approaching 100 percent. Accordingly, in another year or other places, cone moths could prove to be significant pests of noble fir seed. The western conifer seed bug (*Leptoglossus occidentalis* Heidemann) was not observed associated with noble fir cones, though it was a common associate with other tree species at lower elevations.

Counts of insect populations in cone thirds showed that the damaging insects were equally distributed throughout the cones (Table 1). Chalcid populations per cone were positively correlated with both cone length and weight. Lepidoptera and Diptera populations per cone were not correlated with cone length and weight.

TABLE 1. Percent of insect infested seed in noble fir by cone thirds.

Insect species	Cone third infested		
	Top	Middle	Bottom
Megastigmus pinus	17.7	25.7	20.4
Earomyia spp.	11.9	10.4	14.2
Cone moths	7.3	5.0	7.4
Total	32.6	37.0	36.6

Observations showed that insect species are usually identifiable by characteristics of damage, life history features, and appearance and location of immature forms—information useful in developing sampling schemes and control strategies.

Megastigmus pinus (Seed Chalcid)

Females began ovipositing into seeds near the end of pollen flight, just after the cone

bracts completely turned down. The peak period of activity was 24 June to 14 July, with some eggs laid as late as 4 August. Eggs were inserted directly into the seeds through the insect's long ovipositer, which always pierced the cone surface at the lower margin of the bract. Only one larva was observed to develop per seed, but histological evidence suggested that more than one egg was occasionally deposited into a single seed.

The wasp has one generation per year, and the larvae overwinter in the seeds on the forest floor (Hedlin, 1974). Laboratory rearing of infested seeds (cold-treated at 1.5° C for 90 days to break hibernation) suggested that males precede females by about one week during spring emergence. The total emergence period in the laboratory was 25 days, and the sex ratio was 1.2 males per female. Some 40 percent of the infested seeds contained living larvae but did not produce adults. Presumably these insects were in the state of extended diapause and adults would emerge in subsequent years. This is a normal pattern for this species (Hedlin *et al.*, 1980).

Seeds infested by the seed chalcid could not be distinguished from sound seed without dissection or X-ray analysis.

Earomyia barbara and E. longistylata (Cone Maggots)

The two species of fir cone maggots could not be distinguished in terms of larval taxonomy or damage. The larval stages are white, legless maggots, and 8-10 mm long when full-grown; they mine throughout the cone. Feeding by both species leaves darkened empty seed coats with round, frass-free holes, a type of damage unlike that caused by any other associated species.

Both species apparently had one year life cycles, although Keen (1958) reported that extended diapause exists within this genus. The adults began ovipositing in early June, just as the start of pollen flight, and continued until the cone bracts turned down near the end of June. Eggs were deposited between cone bracts, deep within the developing cones. The larvae mined in the cones throughout the summer, burrowing from scale to scale, feeding on seeds. Cone maggots were also observed to be predaceous on other insects encountered in the cones, especially on seed chalcids and gall midge larvae. In early September, before the cones shattered, the larvae left the cones and fell to the forest floor, where they overwinter as pupae (Hedin *et al.*, 1980).

Eucosma sp. (Cone Moth)

Damage caused by the fir cone moth occurred at both study sites but was most frequent at Mary's Peak. The larva is whitish, hairless, 10-15 mm long, and has a dark brown head capsule. The pupa, which is also found in cones, is dark brown and 6-9 mm long. The larval mines are lined with pitch and silk. It was the only cone moth that pushed frass outside the cone.

The moth had one generation per year. Oviposition was not observed but occurred before the first cones were bagged on 9 June, well before pollination. Larval mining and pupation occurred throughout the cone, and the pupae fell to the ground when the cones shattered in October. Because cold treatment of pupae was needed to obtain adults, it appears likely that the insect overwinters in the pupal stage.

Laspeyresia sp. (Seed Moth)

Damage levels by this species were quite variable at the two study sites. Cones could have up to five larvae without significant damage, while all seeds were destroyed in a cone with 35 larvae. Between those extremes, damage was proportional to the number of larvae in a cone. Mature larvae are white to pink, hairless, 8-12 mm long, and have dark brown head capsules. The larvae consumed all the contents of attacked seed, entering and leaving through small holes bored in the seed near the micropylar end. This left a seed coat filled with fine frass, a characteristic unique to *Laspeyresia* and identifiable on X-ray photographs.

Bagging studies showed that eggs were laid before 9 June, and larvae were found in the cones until seed dispersal in the fall. Specific overwintering habits are unknown; but when reared, the insects passed a three month cold storage period as larvae in cocoons.

Dioryctria sp. (Cone Worm)

This insect was found at both study sites and caused general damage to seeds, scales, and bracts. It was uncommon to find more than two larvae in a cone, although one cone had six larvae which completely destroyed all seeds in the cone. Mature larvae were about 20 mm long, hairless, dark pink to green, with dark brown head capsules. Infested cones were filled with coarse reddish to brownish frass.

Oviposition was not observed in the field, but bagging studies and the literature (Keen, 1958) suggest that eggs are laid on conelet bracts in early spring, during the initial stages of cone elongation. Mature larvae left the cones before the cones shattered and apparently pupated on the forest floor. Some adults emerged from rearing without cold treatment, which supports Keen's (1958) suggestion of a partial second generation.

Eupithecia sp. (Cone Looper)

Only two specimens of this looper were found, both at Mary's Peak. The larvae were typically geometrid in shape, light green, and about 20 mm long when full-grown. Damage was similar to that caused by *Dioryctria*; that is, seeds, scales, and bracts were consumed and much coarse frass was produced.

Details of the life cycle are unknown. The larvae pupated inside the cone and apparently dropped to the forest floor when the cones shattered.

Dasineura sp. (Seed Midge)

Feeding by these midge larvae produced a gall on the scale adjacent to the seed, each gall containing one to seven tiny (1- to 3-mm) pink to orange larvae. About 7 percent of the seeds in the study were infested with this midge. Since the insect was rarely associated directly with seed, the damage caused is unknown. Franklin (1974) reports that germinability of galled *Abies* seed is not reduced, but there could be other effects. For example, it was noted in his study that galls in the upper third of noble fir cones (where the seeds are small) often replaced the seeds altogether. Galls also fused the seed to the scale, thus reducing both a seed's capacity to disperse and the efficiency of extraction machinery at seed processing centers.

Gall midge adults oviposit in early June, when the cone bracts are open to receive pollen. Larvae colonize a scale and remain there until the cone shatters in the fall. Winter is spent on the forest floor, probably in the larval stage (Hedlin, 1967).

Cone Resin Midge

This insect was encountered frequently during the study. In the feeding stage it was similar to *Dasineura*, but appeared in clusters of 3 to 20 larvae in a resinous patch between the scale and seed wing. A necrotic spot of tissue developed at the feeding location, but it appeared that damage to seed (if any) was insignificant. The life cycle is unknown but is probably similar to *Dasineura.*

Discussion and Conclusions

The mean seed potential of 733 seeds per noble fir cone found in this study is significantly larger than the 500 seeds per cone reported by Franklin (1974). It must be noted, though, that the data from this study came from 40-year-old trees, which usually have larger cones than old-growth trees.

This study, like other investigations with *Abies* (Franklin, 1974; Keen, 1958) showed that filled seed was rare (0.7 percent) and that the number of unfilled seed was large (63.3 percent). We suspect this partly reflects the poor cone year throughout the region in 1977. Franklin and Ritchie (1970) noted that male strobli are often scarce in poor cone years and suggested that a shortage of pollen in those years could result in a significant number of empty seeds.

An even greater number of unfilled seeds could have been obscured by the 36 percent seed loss we attributed to insect damage. The seed chalcid (*M. pinus*) has been observed to develop in empty seeds as well as in filled seeds.[2] We think that some of the other insects found in noble fir cones, notably *Eucosma* and *Dioryctria,* may feed on empty seeds. Thus, an insect control program might not result in a significant increase in sound seeds, even when insects are abundant, especially in years with poor to medium cone crops.

This study is important because data on and factors affecting noble fir seed potential are scarce. Additional information is needed on temporal and geographic variation. To aid in forecasting seed production, foresters need to know whether lack of pollen is a regular problem or if it occurs only in poor cone years; forecasters also need to know whether insects are feeding on comparable proportions of filled and empty seeds. Some biological measure is needed to establish when insect control will yield practical results and when it will not.

Acknowledgments

We wish to thank the Crown Zellerbach Corporation, Clackamas Managed Forest, for their cooperation in the field phase of this study. We are also grateful for insect identifications by USDA taxonomists at the Systematic Entomology Laboratory, Beltsville, Maryland, specifically George Steyskal, R. G. Gagné, D. C. Ferguson, and Paul M. Marsh.

Literature Cited

Franklin, J. F. 1964. Some notes on the distribution and ecology of noble fir. Northw. Sci. 38(1): 1-13.

———. 1974. Abies. p. 168-183 *in* Seeds of Woody Plants in the United States. U.S. Dept. Agric. Handb. No. 450.

———, and G. A. Ritchie. 1970. Phenology of cone and shoot development of noble fir and some associated true firs. For. Sci. 16(3):356-364.

[2]Pers. comm., Dr. Jerry F. Franklin, Forestry Sciences Laboratory, Corvallis, Oregon 99331.

Hedlin, A. F. 1967. Cone insects of grand fir, *Abies grandis* (Douglas) Lindley, British Columbia. J. Entomol. Soc. B.C. 64:40-44.
———. 1974. Cone and seed insects of British Columbia. BC-X-90, Can. For. Serv., Pac. For. Res. Centre, Victoria, B.C.
———, H. O. Yates III, Cibrian Tovar, and others. 1980. Cone and Seed Insects of North American Conifers. Can For. Serv., U.S. For. Serv., Secretaria de Agricultura y Recursos Hidraulicos, Mexico.
Hermann, F. R., R. O. Curtis, and D. J. DeMars. 1978. Height Growth and Site Index Estimates for Noble Fir in High-Elevation Forests of the Oregon-Washington Cascades. USDA For. Serv. Res. Pap. PNW-243, Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.
Keen, F. P. 1958. Cone and Seed Insects of Western Forest Trees. USDA Tech. Bull. No. 1169.
Mitchell, R. G. 1966. Infestation Characteristics of the Balsam Woolly Aphid in the Pacific Northwest. USDA For. Serv. Res. Pap. PNW-35, Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.
Simak, Milan. 1970. New uses of X-ray methods for the analysis of forest seed. Res. Note No. 23. Dept. of Reforestation, Royal College of For., Stockholm, Sweden.

Received April 7, 1981
Accepted for publication August 24, 1981

Bonnie Heidel

E. Jennifer Christy

and

Amy Jean Gilmartin

Department of Botany
Washington State University
Pullman, Washington 99164

Numerical Phenetic Analysis of Variation in Populations of Poa secunda **Presl. and** Bromus japonicus **Thunb.** (Poaceae)

Abstract

Vegetative and floral morphological characteristics appropriate to the Poaceae were assembled, and variabilities between population samples of two grass species from the steppe of eastern Washington were contrasted using multivariate analyses. The species are a native, perennial inbreeder, *Poa secunda,* and an introduced, annual inbreeder, *Bromus japonicus.* Floral differentiation between populations is highest in *Poa secunda,* while our samples of this species show no differentiation vegetatively. Vegetative differentiation between populations of *Bromus japonicus* is evident but is exceeded by floral differentiation between populations of *Poa secunda.* In both taxa, individuals from more mesic sites showed greater intrapopulation variability than those from the drier sites in *Bromus japonicus* and *Poa secunda.* Within-population variability is higher for vegetative than for floral characters in the mesically growing *Bromus* and the xerically growing *Poa.* Results are compatible with the theory which predicts that the facultative apomict, *Poa secunda,* will show a broader range of adaptive variation than the strictly sexually reproducing apomict, *Bromus japonicus.*

Introduction

Among the native and introduced bromegrasses and bluegrasses prominent in western North America are perennials, annuals, inbreeders, and outbreeders. Variability of sympatric populations of inbreeding, annual, and perennial grasses has not been explored intensively with multivariate analyses. Such studies are of value to both systematists and ecologists. We have quantified the pattern of morphological variability between two steppe grasses. The OTUs (operational taxonomic units) are individual plants sampled from local populations.

The following generalizations form a conceptual framework for predicting patterns of differentiation. Phenotypic plasticity, the individual's responses to environmental stimuli (Cook, 1968), is prevalent over fine-tuned adaptation for introduced, annual species (Iman and Allard, 1965), whereas fine-tuned adaptation predominates in native species (Baker, 1972, 1974; McNeil, 1976). Under stable, recurrent conditions, adaptations which are fixed genetically allow for more permanent, finely tuned responses than does phenotypic flexibility or plasticity, and each type of response is present in both inbreeders and outbreeders (Jain and Bradshaw, 1966). Populations of perennial species show more adaptive variation than annual species because the former would be likely to include individuals of different ages which may have been submitted to different environments in their developmental stages (Hamrick *et al.,* 1979). These authors also suggest that species which reproduce both sexually and asexually show a broader range in adaptive variation than more strictly sexually reproducing ones.

The variation patterns will reflect the fact that vegetative characters respond more directly to the environmental factors, while floral traits are more stable, having evolved in response to strong selection pressures such as for fecundity and have become canalized (Bradshaw, 1965; Stebbins, 1974).

The above generalizations and our observations of the two grass species led to the development and testing of the following three hypotheses. (1) The introduced, annual inbreeder, *Bromus japonicus* Thunb., will vary more vegetatively within and between populations than the native perennial inbreeder (and facultative apomict) *Poa secunda* Presl. (2) Within population variability will be higher with vegetative characters than floral ones, and populations of the perennial, facultative apomict *P. secunda* will display higher interpopulation variation with respect to floral characters than vegetative ones. (3) In addition, because mesic sites permit more "experimentation" by the plants, it is predicted that variability within populations from more mesic sites will exceed that for populations of both species from the more xeric habitats.

Application of numerical phenetic techniques has flourished in systematics (Crovello, 1970; Sneath and Sokal, 1973) in which the units of comparison are taxa (e.g., Gilmartin, 1969a, 1974; Jensen and Eshbaugh, 1976; Adams, 1977; Parker *et al.*, 1979; Jacobsen, 1979) or sample sets within the species circumscription (Ellis *et al.*, 1971; Gilmartin, 1977; Riggins *et al.*, 1977; Wilkin, 1978). Related techniques have been applied in ecology for delimiting and evaluating communities (Goodall, 1973; Bray and Curtis, 1957; Williams and Lambert, 1966; Grigal and Goldstein, 1971). Ellis *et al.* (1971) employed large samples (many OTUs from each of seven populations and nine variables) in a biometric analysis of colonization of the introduced *Poa annua* in Australasia. They concluded that while *Poa annua* has been considered to be an inbreeder, their analyses suggest outbreeding. Considerable differences in intrapopulational variabilities among the populations were shown, and the degrees of similarities between members of pairs of different populations in terms of generalized distance varied more than 100 percent in some cases.

Methods and Materials

The two prairie grasses under study occur throughout the Palouse steppe in southeastern Washington and are widespread elsewhere in the Pacific Northwest. *Poa secunda* is a common native species (Weaver, 1917; Daubenmire, 1970) and flowers early. It is a facultative apomict (Hartung, 1946), as are other species of the scabrellae complex (Clausen and Hiersey, 1958), and is typically cleistogamous. *Bromus japonicus* was introduced from Asia and was not recognized in the regional flora (St. John, 1963) until recently (Hitchcock *et al.*, 1969). It is among the latest flowering of the annual bromes in the area (Hulbert, 1955) and is usually cleistogamous (Hitchcock *et al.*, 1969; Smith, 1944). Thus, both species tend to be inbreeders.

The sampling area for each population of *Bromus japonicus* and *Poa secunda* was less than 10 m^2. All four populations are on the same hilly tract five miles west of Colton, Whitman County, Washington. The *Bromus* and *Poa* populations Bx and Px are growing together on a xeric, south-facing slope of the *Agropyron spicatum-Poa secunda* habitat type (Daubenmire, 1970). *Poa* population Pm is on a more mesic north-facing slope, and Bm is growing at a mesic fencerow site between adjacent wheatfields where moisture accumulates. The latter two sites are the *Festuca idahoensis-Symphoricarpos*

albus habitat type (Daubenmire, 1970). No *B. japonicus* grows at the Pm site, and *P. secunda* does not occur at the Bm site.

Population samples consisted of 12 solitary annual culms of *B. japonicus* collected late in the fruiting stage in October 1978. The two sampling sites (Bx and Bm) were approximately 200 m apart. Twelve caespitose plants of the perennial *P. secunda* were sampled from different clumps to increase the likelihood of each culm belonging to a different clone. These two sampling sites (Px and Pm) were approximately 50 m apart.

The adequacy of the 12-member sample for estimating population variability with a large number of characters has been substantiated among several plant families (Gilmartin, 1974), for *Bromus tectorum* (Bookman, 1980), *Agropyron spicatum* (Dobrowolksi, 1979), and for two species of *Festuca* with a somewhat different character-list (Belsky, 1979). A more extensive character list for the Poaceae is that of Clifford and Goodall (1967).

Data were recorded for each plant with 64 morphological characters applicable to the Poaceae (Dobrowolski, 1979). Twenty vegetative characters (leaf, ligule, culm, and rhizome characters) and 44 floristic characters (inflorescence, spike, and spikelet characters) were treated as character subsets. The ratios of the number of quantitative to qualitative characters were 3:7 for the vegetative set and 1:2 for the floristic set. All characters were scored in one of five mutually exclusive character-states, the mean number of states being three. Data were standardized to a range of 0 to 1 (Crovello, 1963) to calculate phenetic distances from which were calculated the summary statistics, mean phenetic distance (MPD), standard deviation (SD), and coefficient of phenetic variation (CVD). No *a priori* character weighting was applied.

First, principal components analysis (PCA) using NT-SYS (Rohlf *et al.*, 1974) was conducted to determine if the conspecific populations are distinct. It was based on characters which vary between the conspecific population samples; for *Poa* there were six vegetative and eleven floristic; for *Bromus*, eight vegetative and nine floristic. PCA was performed on a product moment correlation matrix. The first three factors were computed.

Second, discriminant analysis on *Bromus* and separately on *Poa* was applied to identify major differences between populations. While not combined in analysis, results are presented on one axis to facilitate comparisons between populations. A maximum of three best discriminating characters delimited the canonical axis, representing a scale of collective character-states. Individual species samples were aligned along the axis (Fig. 2). The best discriminators were determined, and the inter-population distances were compared between species.

Third, phenetic variation was quantified to compare variation within and between conspecific populations. Each population and both pairs of conspecific populations were treated as datasets. Datasets were condensed, and the summary statistics were computed with the DISTA program (Gilmartin, 1969b), which also indicates the actual number of characters employed for each OTU x OTU comparison.

Phenetic distances were computed as the negative log to the base 2 of the similarity index (Rogers and Flemming, 1964). This is a log transformation of the resemblance coefficient (distance) and not of the data, as is more typical. The phenetic distances become new variates; the mean phenetic distance and standard deviation were calculated

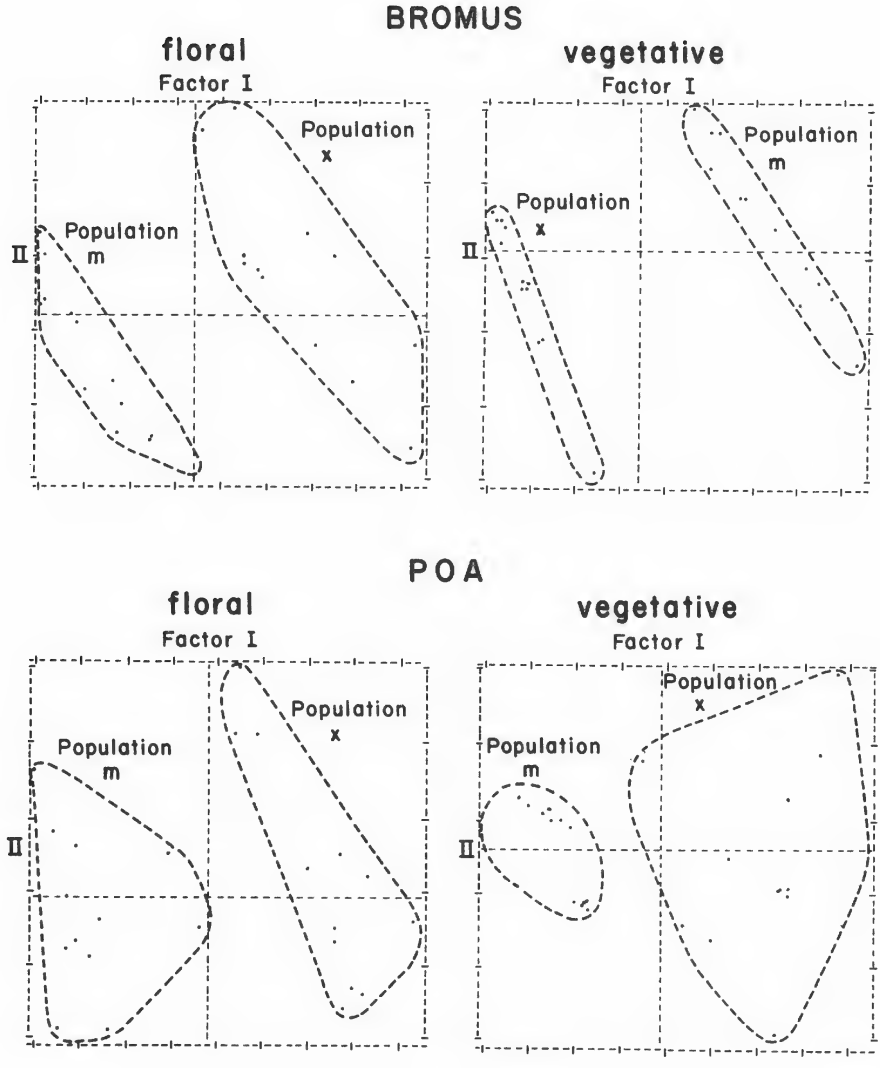


Figure 1. *Bromus japonicus* and *Poa secunda* samples on the first and second axes of a principal components analysis plot using the available 8 vegetative and 9 floristic characters for *Bromus* and 6 vegetative, 11 floral characters in *Poa*. Population X is the xeric site, population M is the mesic site. Proportions of total variance accounted for by each axis are: *Bromus* vegetative dataset: Factor I = 56%, Factor II = 14%, *Bromus* floral dataset: Factor I = 67%, Factor II = 14%. *Poa* vegetation dataset: Factor I = 55%, Factor II = 23%, *Poa* floral dataset: Factor I = 55%, Factor II = 22%.

from a matrix of phenetic distances between all sample members within each dataset. The MPD represents the central tendency of the phenetic dissimilarities, while the SD represents the degree of heterogeneity of the dissimilarities among members of the dataset.

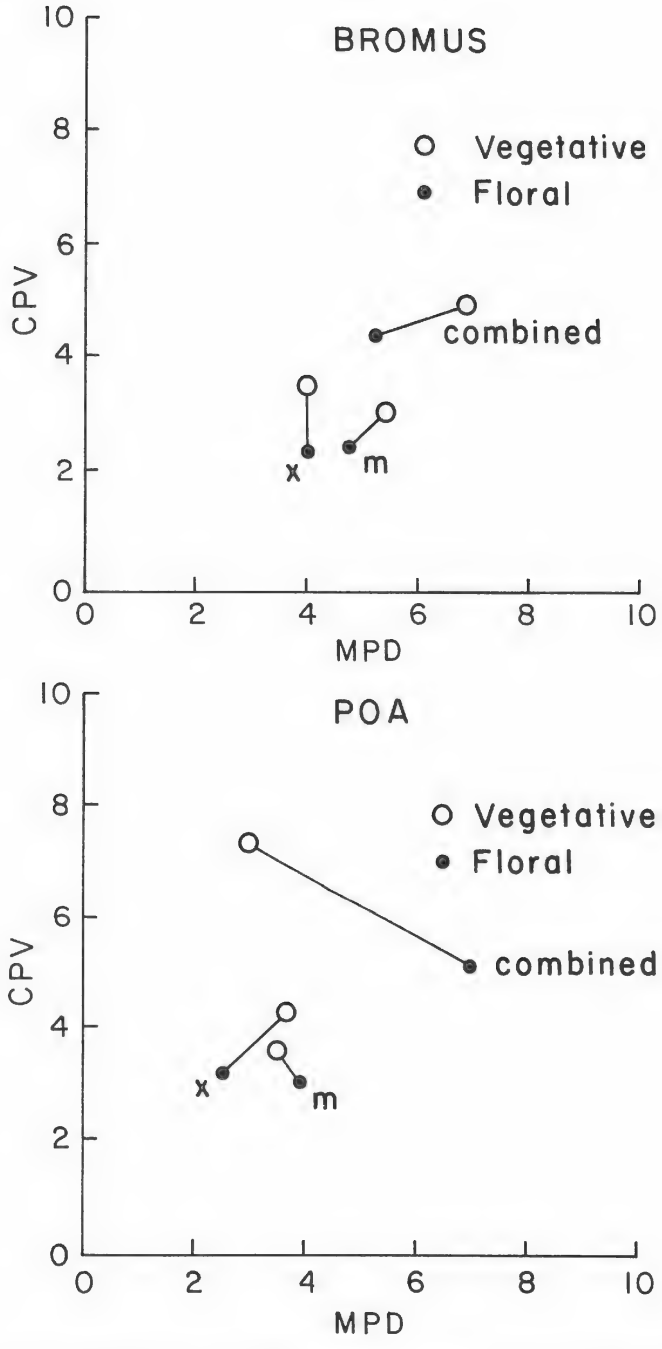


Figure 2. *Bromus japonicus* and *Poa secunda* population members plotted on axes from discriminant analysis using those characters which best discriminate between populations of the species.

A coefficient of phenetic variation (CPV = SD/MPD) was calculated to compensate for scale differences of the MPD when comparing both mean and deviation (Gilmartin, 1974). Were it our goal to discriminate between entities, some other method, such as Mahalanobis D^2, would be appropriate. However, we wish to quantify over all relative amounts of dissimilarity based upon a considerable number of characteristics, rather than test whether two populations are different. The CPV/MPD were plotted for each dataset, displaying the central tendency of variation (the magnitude of the differentiation) and the dispersal (relative degree of uniformity of the dissimilarities among the OTUs). In order to estimate the degree of overall differentiation between two populations, the MPD within each population sample was compared with that obtained from two combined populations. Population pairs which have differentiated will sharply differ in their individual and pooled MPD values. Two populations which have differentiated slightly (or having diverged morphologically, once more have converged) will show little difference in MPD values obtained with pooled and individual samples. However, two populations not distinct in their pooled versus individual MPD values are not necessarily undifferentiated. The two populations may vary in opposing directions, and the counteractive effects may produce a pooled MPD very close to the individual population's MPDs. Such a situation, however, becomes evident if the SDs obtained with pooled and individual samples differ sharply—i.e., if the combined population sample has a much higher SD (less uniformity) than either of the individual samples.

By plotting the CPV against the MPD, a progression of variability (both in terms of magnitude (MPD) and dispersal (SD)) is represented going from the lower left to upper right. While Gilmartin (1980) has done log transformations of such axes in order to portray the linear progression of magnitudes of variation and the dispersal (heterogeneity) of variation within taxa of several categories from species to family, such a transformation is less helpful here because only two levels of variation are included, population and species.

The importance of vegetative and floral variation within and between populations was determined by obtaining the MPD and SD with vegetative and floral characters separately. The presentation technique is modified from Gilmartin (1974) to emphasize character subsets rather than taxonomic levels.

Results

Figure 1 shows the plots for the two factors of PCA which removed at least 70 percent of the variance. The highest character loadings, analogous to correlations between variables and the factor, are shown for Factor I and II in Table 1. The populations of *B. japonicus* (Fig. 1) appear to be more distinct from one another with floral or vegetative characters than the *P. secunda* populations. Ordination accuracy was evaluated by comparing the distances in multidimensional phenetic space with the distances in three-factor space; in all cases, the correlations exceeded 0.95 (reconstructing the original matrix).

Conspecific populations of each species are distinct with respect to the few best discriminating characters (three characters for *B. japonicus* and two for *P. secunda*), but the *B. japonicus* populations showed better separation (Fig. 2). The *B. japonicus*

TABLE 1. Principal component factor loadings obtained with four datasets, floral and vegetative character-sets of **Bromus japonicus** and **Poa secunda**[a]. The first two factors explain at least 70 percent of the correlations.

B. japonicus		**P. secunda**	
	Floral Characters		
Factor I loadings (9[b])		Factor I loadings (11[b])	
Inflorescence length	0.94	Lemma length	0.93
Inflorescence diameter	0.92	Shape of first glume apex	0.92
Branch length	0.90	Number of florets per spike	0.89
Lemma texture	-0.88	Number of spikelets per node	**0.75**
Glume maximum length	-0.87	Length of inflorescence	0.73
Glume maximum width	-0.84	Branch length	0.44
Length of internodes	0.82		
Number of spikelets/node	0.52		
Factor II loadings		Factor II loadings	
Number of spikelets/node	-0.57	Length of internodes	-0.84
Glume maximum width	-0.44	Inflorescence diameter	0.82
Glume maximum length	-0.42	Branch length	-0.80
		Inflorescence length	-0.59
	Vegetative Characters		
Factor I loading (8[b])		Factor I loadings (6[b])	
Culm height	0.91	Leaf-blade length maximum	0.94
Culm degree of hollowness	0.86	Leaf-blade width maximum	0.93
Leaf-blade length	0.84	Culm height	0.83
Culm diameter	0.78	Leaf-sheath indumentum type	-0.70
Ligule diameter	0.73	Ligule length	0.70
Culm pulvinus presence	0.44	Culm diameter	0.36
Factor II loadings		Factor II loadings	
Leaf-blade width	-0.84	Degree stoloniferous	-0.84
Culm degree of hollowness	0.43	Ligule length	0.40

[a]The correlation matrices upon which the analyses were based are deposited with the Ownbey Herbarium, Washington State University.

[b]Number of characters available for the analysis.

population discriminators were lemma length, glume length, and glume width. The *P. secunda* population discriminators were glume width and leaf-blade length.

Variation differences using all 20 vegetative and 44 floristic subsets of characters were used in order to sample two kinds of overall divergences. Variabilities were compared by plotting their CPV and MPD values (Fig. 3). The vegetative subset in all cases shows a higher value in CPV than does the floral subset. However, the standard deviation (dispersal of the distances between the OTUs) of Pm is smaller for the combined *P. secunda* population's vegetative set than the floral subset (Table 2). This finding is also evidenced in Fig. 3 by the reversal in the slope from floral to vegetative of the line depicting combined *P. secunda* populations. In one case, *Poa secunda* combined populations, the slope differs significantly from zero.

The relative amounts of differentiation between conspecific populations are shown by the summary statistics for all datasets in Table 2, and change or difference in SD

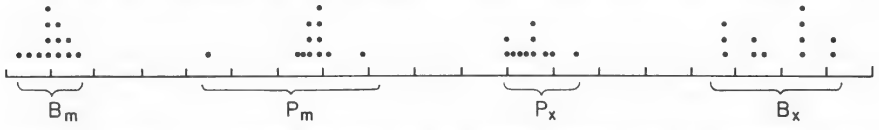


Figure 3. Variability of *Bromus japonicus* and *Poa secunda* datasets using all characters. The ordinant is the coefficient of phenetic variation (CPV), the abscissa is the mean phenetic distance (MPD), each multiplied by a factor of 10.

TABLE 2. Overall variability within and between conspecific populations of **Bromus japonicus** and **Poa secunda** using floral and vegetative subsets of 44 and 20 characters to obtain the MPD (mean phenetic distance), SD (standard deviation) and CPV (coefficient of phenetic variation). Population X is the xeric site, population M is the mesic site.

	B. japonicus		P. secunda	
	Floral	Veg.	Floral	Veg.
Population X				
MPD	0.40	0.40	0.25	0.36
SD	0.10	0.14	0.08	0.15
CPV	0.25	0.35	0.32	0.42
Population M				
MPD	0.48	0.53	0.39	0.36
SD	0.12	0.17	0.12	0.13
CPV	0.25	0.32	0.30	0.36
Combined populations				
MPD	0.52	0.67	0.69	0.31
SD	0.23	0.34	0.36	0.23
CPV	0.44	0.50	0.52	0.74
SD from combined populations minus maximum SD within populations	0.11	0.17	0.24	0.08

from within to between samples is given in the last row. For example, 0.11 is the difference between the SD within and between populations of *B. japonicus* with floral data. The degree of differentiation seen in vegetative and floral features is greater in *P. secunda* than in *B. japonicus*.

Discussion

Hypotheses were only partly supported by the data. For clarity, these will be discussed separately under (A) within population variability (anagenesis) and (B) between population variability (cladogenesis). One of the most useful plots is Fig. 3, which portrays the variability within as well as between conspecific populations employing 20 vegetative and 44 floral traits. The techniques of numerical taxonomy are valuable to ecologists as a means of quantifying descriptive relationships within and between populations. It is clear from Table 2 and Fig. 3 that the overall intra-population variation for *P. secunda*, regardless of character-set, is less than that for *B. japonicus*; that vegetative characters are as variable or more so than floral ones; and that mesic populations vary more than xeric ones. We have applied some methods appropriate to questions concerning relative degrees of overall intrapopulational variability and divergence between conspecific populations. We are much less interested here in discriminating populations. Generalized distance, which is designed to help distinguish populations, is inappropriate to our questions and our datasets, which lack multivariate normality.

A. Within Population Variation, Anagenesis

1. An introduced, annual inbreeder, *B. japonicus*, will vary more than the native, perennial inbreeding facultative apomict *P. secunda*. Using 20 vegetative and 44 floral traits, some of the differences between the two species show the predicted trend. With floral information, variability of Bx (MPD = 0.40, SD = 0.10) is 38 percent higher than Px (MPD = 0.25, SD = 0.08). A biologically interesting difference is considered to be at least 15 percent (Gilmartin, 1974; Bookman, 1980). Florally, the variabilities

did not differ particularly between Pm and Bm, but vegetatively they did differ. Specifically, Bm showed variabilities 32 percent higher in MPD (0.53) than Pm (0.36), and Bm's SD (0.17) was 42 percent higher than Pm's SD (0.13). Other differences are within a few percentage points of 15 percent and are not considered because they are likely the result of sampling error. The differences between Bx and Px are the largest and among the most interesting because these two populations were growing together on the same habitat type, a south-facing slope. The drier site produced a similar amount of vegetative response for both species, but there was less floral variation for *P. secunda* than for *B. japonicus*. We will return to this point later.

Summary statistics employ 22 and 44 characteristics for the vegetative and floral subsets, respectively, whereas the PCA used no more than 11 characters. The algorithms for the PCA and discriminant analysis (DA) are designed to use only variables; only a few traits vary within and between conspecific populations. In addition to the degree of variation of each of the variables, the summary statistics incorporate the PROPORTION of the total character set which actually varies, while PCA does not take into account differences in the proportion of characters which vary. For example, 11 out of 44 floral traits vary in *Poa* and 9 vary in *Bromus*. Six out of 20 vegetative traits vary in *Poa*; eight vary in *Bromus*. The summary statistics incorporate the fact—e.g., that in *Poa* 6/66 or 1/11 of the characters vary. Not only do the summary statistics afford a more unbiased estimate of overall variability than PCA, but they also calibrate the variability for population samples relative to other taxa. Our results can be compared with results derived by using a similar character list. For example, Dobrowolski (1979) found that in 15 paired comparisons among populations of *Agropyron spicatum* (Pursh) Scribn., six of the MPD values for vegetative characters were at least 30 percent greater than the MPD values for floral subsets while the other nine were about equal.

2. Populations of the introduced annual *B. japonicus* are expected to show greater overall variability and difference in vegetative characters than in floral ones. Neither the Bx nor Bm population appears to show appreciably greater vegetative than floral variation (Fig. 2; Table 2).

3. Vegetative traits vary more than floral traits. Considering both the magnitude of variability (MPD) and the dispersal of the dissimilarity values (SD), this conclusion is supported by our data (Fig. 3; Table 2). In all cases the vegetative subsets show as high or higher variability than the floral traits.

4. In each species, individuals from the more mesic habitats will be more variable than individuals from the more xeric habitats. While the Pm population was substantially more variable than the xeric Px population for floral characters (Table 2, Fig. 3), the same cannot be said for the vegetative subset of *P. secunda*. Both vegetatively and florally, the Bm population was more variable than the Bx populations; vegetative characters varied the most. Thus, the *Bromus japonicus* mesic population varied more vegetatively, and the *Poa secunda* mesic population varied more florally.

B. Variation between Populations, Cladogensis

This type of variability is of great interest to taxonomists involved in circumscription of taxa and interpretations of the processes of speciation. Each of the hypotheses stated

in the introduction will be dealt with as in part (A) above but will also be considered with regard to interpopulation variability.

1. An introduced, annual inbreeder, *B. japonicus* will show more interpopulation variability than the native perennial, *P. secunda.* Results of each of the three methods (PCA, DA, and summary statistics) are pertinent. The PCA plots (Fig. 1) of the first two factors show the *Bromus* populations to be somewhat more distinct for both vegetative and floral traits than the *Poa* populations. The best distinction between *Bromus* populations is based on vegetative traits. The results with PCA with 11 or fewer variates are supported by the summary statistics obtained with 20 and 44 characters.

The relationship (Kluge-Kerfoot phenomenon) between variability within populations and divergence between population has been shown to be significant (Kluge and Kerfoot, 1973; Sokal, 1976) for individual characters for a number of vertebrate and invertebrate taxa. It is not known yet if this holds for plants or for overall variability. Our results with overall variabilities show discrepancies from this association. Table 2 shows the change in CPV and MPD from individual to combined populations for *Poa* with floral traits, and the decrease in MPD with vegetative traits. There is little vegeative change but great floral change for *P. secunda.* This point is illustrated in Fig. 2 by the proximity of the open circles (vegetative subset) for both Px and Pm and the lack of any increase in PMD from within to between populations. Table 2 and Fig. 3 do show, however, that the SD of the *Poa* floral samples differs from within to between populations. The hypothesis must be considered supported by the data only for floral traits, since floral traits of the *Poa* populations are more differentiated than the *Bromus* samples. The next higher differentiation is between the two Bx and Bm populations vegetatively.

2. Populations of *B. japonicus* differ more in vegetative characters than in floral ones; the converse is true for *P. secunda.*

3. Vegetative traits vary more between populations than floral traits. This is true for *B. japonicus* and false for *P. secunda.*

4. Hypothesis number 4 is only applicable to within populational variability and is discussed under (A).

In summary, we find different responses to similar and to differing environments in the two evolutionary lines, with *Poa* differentiating more florally and *Bromus* differentiating more vegetatively.

The high overall variability within the introduced *B. japonicus* populations in both sites was expected, but the greater differentiation between *Poa* populations is especially interesting. While both species are inbreeders, only *P. secunda* is a facultative apomict; this apomixis should result in differentiation between local populations. The fact that it is demonstrated more by floral traits than vegetative ones also suggests an evolutionary derivation for this distinction rather than strict plasticity. In addition, older populations are expected to show greaer interpopulational differentiation. Populations of *P. secunda,* a native of the Pacific Northwest, differ more between populations than do the populations of the introduced *B. japonicus.*

Whereas we hypothesized that the perennial nature of *P. secunda* would impose greater variability among individuals within populations due to individuals being of different ages as suggested by Hamrick *et al.* (1970), we do not find any evidence of

this. The explanation could be that this response, while present, is swamped by other factors, or indeed that all of the individuals of the *P. secunda* populations which were sampled were approximately of the same age, a phenomenon which often occurs among some of the perennials of the Pacific Northwest because of grazing practices.

Factor II of PCA (Fig. 1) plays little or no part in grouping together members of a population sample, but Factor I does. We feel that an elongation factor is evidenced by Factor I loadings for floral traits of both species; e.g., lengths of inflorescence, branches, and internodes. Factor I includes some of the variables such as a plant height and inflorescence size used by Iman and Allard (1965) to quantify genetic information (in a study of wild oats). Factor I could be thought of simply as a size factor, as often occurs for the first axis of PCA. Beyond the size element within Factor I, there are in *Poa* a meristic component (number of florets, number of spikelets) and glume apex shape which play a role. These latter three traits are particularly developmental or meristematic and more evident in *P. secunda* than in *B. japonicus.*

The drier sites (Px, Bx) were accompanied by less variability within all datasets, especially for the *Poa* floral set. This is interpretable by recalling that *P. secunda* is a facultative apomict and that variants may survive in the more favorable Pm site and not in the Px site. Vegetatively, the responses of the two *Poa* populations were very similar. As pointed out by Jain and Bradshaw (1966, p. 436), localized differentiation is entirely explicable by a species having ". . . the ability to develop the relevant characters by processes of conditioning in the vegetative phase." Such conditioning (direct responses during the lifetime of the individual) would be a much more potent force in a perennial than in an annual species.

In conclusion, populations of both species have differentiated, but *Poa* demonstrated greater floral differentiation. We interpret this as an evolutionary response. Within-population variability is somewhat greater in *Bromus* than *Poa*, regardless of the character space. We interpret this as a manifestation of acclimation or plasticity within the *Bromus* populations. The PCA plots, which were based on small sets of characters (6-11), were useful for comparing OTUs; but the summary statistics, which include many more characters (20-44) and incorporate an estimate of overall variability (the proportion of the characters which vary out of the total subset of characters being used), provide a calibration of our results for comparisons with results of other studies.

Questions which remain unanswered concern relative influences of: reproductive systems; annual versus perennial habit; and the length of establishment of the populations. Do long-established populations of the annual *Bromus japonicus* growing as a native in Europe show the same degree of interpopulation floral differentiation as the American native populations of the perennial, facultative apomict, *Poa secunda*? While we found that parapatric populations differentiate as predicted (Jain and Bradshaw, 1966), it will be interesting to learn if parapatric populations of *Poa secunda* not from contrasting moisture regimes will show the same degree of floral differentiation. Using the described techniques, the foregoing questions can be answered as well as others; e.g., do allopatric populations of *Poa secunda* in the same and different moisture regimes show the same degree of floral differentiation, and if not, by how much do they differ, and which characters vary? Herein, we have been able to quantify the differing responses of populations of two grass species, and the answers we have provided may have applicability to many species.

Acknowledgments

We thank the following people who critically read drafts of the manuscript: T. J. Crovello, J. Felsenstein, D. Goodall, J. Maze, and J. McNeill. M. Barkworth provided background information. Research was supported by NSF grants DEB 76-82292 and SER 77-11609 with AJG as principal investigator.

Literature Cited

Adams, R. P. 1977. Diurnal variation in volatile terpenoids of *Juniperus scopulorum* (Cupressaceae). Ann. Mo. Bot. Gard. 64: 184-209.

Baker, H. G. 1974. The evolution of weeds. Ann. Rev. Ecol. Sys. 5: 1-24.

———. 1975. Human influences on plant evolution. Econ. Bot. 26:32-43.

Belsky, J. A. 1979. Determinants of Ecological Amplitude in *Festuca idahoensis* and *Festuca ovina.* Univ. of Washington. Ph.D. thesis.

Bookman, P. 1980. Variation in *Bromus tectorum* (Poaceae) in Eastern Washington. Madrono 27:36-42.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genetics 13:115-155.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest community of southern Wisconsin. Ecol. Monogr. 27:325-349.

Clausen, J., and W. H. Hiesey. 1958. Experimental Study on the Nature of Species. IV. Genetic Structure of Ecological Races. Carnegie Institute of Washington Pub. No. 615.

Clifford, H. T., and D. W. Goodall. 1967. A numerical contribution to the classification of the Poaceae. Aust. J. Bot. 15:499-519.

Cook, C. D. K. 1968. Phenotypic plasticity with particular reference to the amphibious plant species, pp. 97-110 *in* Heywood, (ed.), Modern Methods in Plant Taxonomy.

Crovello, T. J. 1968. Quantitative Taxonomic Studies in the Genus *Salix* Section *stichensis.* Univ. of California Pub. in Bot. No. 44.

———. 1970. Analysis of character variation in ecology and systematics. Ann. Rev. Ecol. Sys. 1: 55-98.

Daubenmire, R. 1970. Steppe Vegetation in Washington. Wa. Ag. Exp. Sta. Tech. Bul. No. 62.

Dobrowolski, J. P. 1979. A Numerical Taxonomic Analysis of *Agropyron spicatum* (Pursh) Scribn. and Smith with Special Reference to Ecotypic Variation. Washington State Univ. M.S. thesis.

Ellis, W. M., B. T. Lee, and D. M. Calder. 1971. A biometric analysis of populations of *Poa annua* L. Evolution 25:29-37.

Gilmartin, A. J. 1969a. The quantification of some plant-taxa circumscriptions. Amer. J. Bot. 56: 654-663.

———. 1969b. Numerical phenetic samples of taxonomic circumscription in the Bromeliaceae. Taxon 18:378-392.

———. 1974. Variation within populations and classification. Taxon 23:523-536.

———. 1977. Variation and distribution. Taxon 22:223-225.

———. 1980. Variation within populations and classification. II. Patterns of variation within Asclepiadaceae and Umbelliferae. Taxon 29:199-212.

Goodall, D. W. 1953. Objective methods for the classification of vegetation I. The use of positive interspecies correlation. Aust. J. Bot. 1:39-63.

Grigal, D. F., and R. A. Goldstein. 1971. An integrated ordination classification analysis of an intensively sampled oak-hickory forest. J. Ecol. 59:481-592.

Hamrick, J. L., Y. B. Linhart, and J. B. Mitton. 1979. Relationship between life history characteristics and electrophoretically detectable genetic variation in plants. Ann. Rev. Ecol. Syst. 10:173-200.

Hartung, M. E. 1946. Chromosome numbers in *Poa, Agropyron,* and *Elymus.* Amer. J. Bot. 33: 516-531.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1969. Vascular Plants of the Pacific Northwest. Univ. of Washington Press, Seattle.

Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecol. Monogr. 25:181-214.

Iman, A. G., and R. W. Allard. 1965. Population studies in predominantly self-pollinated species. VI. Genetic variability between and within natural populations of wild oats, *Avena fatua* L., from differing habitats in California. Genetics 51:49-62.

Jacobsen, T. J. 1979. Numerical analysis of variation between *Allium cernuum* and *Allium stellatum* (Liliaceae). Taxon 28:517-523.

Jain, S. K., and A. B. Bradshaw. 1966. Evolutionary divergence among adjacent Plant populations. Heredity 21:407-441.

Jensen, R. J., and W. H. Eshbaugh. 1976. Numerical taxonomic studies of hybridization in *Quercus* I. Populations of restricted areal distribution and low taxonomic diversity. Syst. Bot. 1:1-10.

Kluge, A., and W. Kerfoot. 1973. The predictability and regularity of character divergence. Amer. Nat. 107:426-442.
McNeill, J. 1976. The taxonomy and evolution of weeds. Weed Res. 16:399-413.
Parker, W. H., G. E. Bradfield, J. Maze, and S. C. Lin. 1979. Analysis of variation in leaf and twig characters of *Abies lasiocarpa* and *A. amabilis* from north-coastal British Columbia. Can. J. Bot. 57:1354-1366.
Riggins, R., R. A. Pimentel, and D. R. Walters. 1977. Morphometrics of *Lupinus nanus* (Leguminosae). I. Variation in natural populations. Syst. Bot. 2:317-326.
Rohlf, F. J., T. Kispaugh, and D. Kirk. 1974. Numerical Taxonomy System of Multivariate Sta. tistical Programs. State Univ. at Stony Brook, New York.
Rogers, D. J., and H. Fleming. 1964. A computer program for classifying plants. Bio. Sci. 14:14-28.
St. John, H. 1963. Flora of Southeastern Washington. Outdoor Pictures, Escondido, CA.
Sneath, P. H. A., and R. R. Sokal. 1973. Numerical Taxonomy. W. H. Freeman and Co., San Francisco.
Sokal, R. 1976. The Kluge-Kerfoot phenomenon reexamined. Amer. Nat. 110:1077-1091.
Stebbins, G. L. 1974. Flowering Plants, Evolution above Species Level. Belknap Press, Cambridge.
Smith, D. C. 1944. Pollination and seed form in grasses. Jour. Ag. Res. 68:79-95.
Weaver, J. E. 1917. A study of the vegetation of southeastern Washington and adjacent Idaho. University Studies, Vol. XVIII No. 1:2-88.
Wilkin, D. H. 1978. Vegetative and floral relationships among western North American populations of *Collomia linearis* Nutt. (Polemoniaceae). Amer. J. Bot. 65:869-901.
Williams, W. T., and J. M. Lambert. 1966. Multivariate methods in plant ecology VI. Comparisons of information-analysis and association-analysis. J. Ecol. 54:635-664.

Received June 9, 1980
Accepted for publication September 2, 1980

Paul E. Schroeder
Brooks McCandlish
Richard H. Waring
and
David A. Perry
Department of Forest Science
Oregon State University
Corvallis, Oregon 97331

The Relationship of Maximum Canopy Leaf Area to Forest Growth in Eastern Washington

Abstract

Because forests in eastern Washington often exhibit stocking levels significantly below those predicted by standard yield tables, a method was sought to better estimate potential forest-site productivity. Maximum canopy development, expressed as layers of leaves per unit of ground area, or Leaf Area Index (LAI), was more closely related to maximum current stemwood production than was site index alone or a combination of site index, basal area, and age; however, the relationship was not regionally independent. A ratio of annual stemwood production per unit of leaf area, derived from measurements of radial growth and sapwood thickness, was responsive to changes in canopy density within a particular forest but was not sufficiently sensitive to estimate maximum potential LAI.

Introduction

Site index, defined as the height of dominant trees at a particular age, is often chosen as an empirical measure of the productive capacity of a forest site. Potential wood production can be estimated from empirical yield tables for a specific site index. An inherent assumption for such tables is that all areas with the same site index have equal productivity and support the same number of trees per unit area at a comparable age. This assumption, however, becomes invalid if the canopy leaf area that can be maintained varies. In arid regions particularly, where each tree requires more space to fulfill its moisture requirements, the resulting forests have less than normal stocking (Wilkstrom and Hutchinson, 1971; MacLean and Bolsinger, 1973). Normal yield tables overestimate productivity in such situations to the extent that stocking is below that predicted.

An alternative approach to estimating productivity was examined in this study. We tested a general premise that canopy leaf area might be directly related to the productivity of mixed stands of conifers across regions (Madgwick and Olson, 1974; Albrektson *et al.*, 1977; Gholz, 1979) by examining fully stocked stands which exhibit some recent mortality of suppressed trees.

The overall goal of our research—to develop a method to estimate potential forest-site productivity—comprised two specific objectives: (1) testing the hypothesis that a regionally independent relationship exists between Leaf Area Index (LAI), the foliage surface area per unit of ground area, and productivity; and (2) estimating the maximum possible LAI for a site by extrapolating to the point where wood production per unit of

leaf area approaches zero as the forest canopy closes (Waring *et al.*, 1980; Waring *et al.*, 1981).

Study Area

The study area encompassed nearly all forested lands in Washington state located east of the crest of the Cascade Mountains. Excluded was the northernmost segment of Umatilla National Forest extending into the extreme southeastern corner of the state, since a vegetation analysis with predictions of forest productivity had already been completed there (Hall, 1973; MacLean and Bolsinger, 1973).

A wide range of environments is encountered across the area. Forests range in elevation from 600 to over 1800 m. Mean annual precipitation is approximately 2500 mm at the crest of the Cascades, but only about 250 mm at the lower forest boundary; considerable snow accumulates near the crest with lesser amounts at lower elevation. Temperatures vary, and cold winters are common throughout the eastern part of the state. In general, the growing season is cool and moist at higher elevations and hotter and drier at lower elevations (Franklin and Dyrness, 1973). The interaction between regional climate and local topography leads to a great diversity of forest types and a range in productivity of from < 2 to > 18 m^3 of stemwood $ha^{-1}yr^{-1}$.

Procedures

Stands were selected on the basis of two criteria: full stocking and absence of disturbance. We examined suppressed understory trees to assure that some mortality, indicating full stocking, had occurred within the last decade and evaluated disturbance by inspecting for stumps, skid roads, and evidence of recent fire; in some cases, undisturbed stands were impossible to locate. In these instances, we estimated whether the disturbance had occurred far enough in the past to allow probable recovery of both the overstory and understory trees. Because our primary emphasis was to test the more general hypothesis across regions, an effort was made to distribute sample plots sparsely over the entire study area, thereby including representatives of the whole spectrum of topographic, climatic, and forest types.

Initially located from maps, where roads crossed major climatic zones, stands were surveyed along transects similar in aspect, elevation, and vegetation; four to six sample points per stand were established along each transect. Care was taken to avoid microsites such as seeps and rock outcrops. Trees were sampled at each point with a metric 7-factor wedge prism and their diameters at breast height (DBH) recorded. Sapwood thickness, used to estimate LAI, and radial stem-growth increment for the previous five years were determined from increment cores extracted at breast height from the uphill side of each tree; the last five-year increment was averaged to avoid distortions from anomalies in a single year's growth. For each stand, total height and age at breast height were recorded for a subsample selected either from a range of diameters or from dominant trees appropriate for site-index determination.

A number of thinned stands were sampled to provide a wider range of canopy leaf areas on individual sites than occurred naturally so that the change in wood production per unit of leaf area as the canopy closes could be examined.

Analysis

Cross-sectional sapwood area at breast height was calculated from sapwood thickness and DBH measurements; the sapwood was assumed to be symmetric. Although the analyses required to relate sapwood area directly to leaf area had not been completed for most species east of the Cascades (east side) at the time of this study, Brown (1978) had developed equations to estimate foliage biomass as a function of DBH for five coniferous species in the intermountain region (Table 1). For each of these species regressions were fitted by least squares to the model:

$$\ln (DBH) = b_0 + b_1 \ln (SA) \quad (1)$$

where SA = sapwood area in square centimeters.

These regressions, transformed and corrected for bias as suggested by Baskerville (1972), were substituted in Brown's equations. Foliage biomass was converted to projected (one-sided) leaf area by multiplying by factors from Gholz *et al.* (1976), Anderson *et al.* (1978), and Smith (1980) (Table 1). Four other coniferous species were common on the plots but no sapwood relationships with foliage were avaiable. For these, foliage biomass was estimated directly from DBH and then converted to leaf area (Table 2). Recently we have found that linear relationships for all these species exist if sapwood area is measured at the base of the crown. The curvilinear nature of equations in Table 1 result from taper in sapwood between DBH and the crown (R. H. Waring, P. Schroeder, and R. Oren, unpublished manuscript, Oregon State Univ., Forest Res. Lab). LAI was

TABLE 1. Equations for estimating projected leaf area (LA) in square meters from cross-sectional sapwood area (SA) in square centimeters at DBH. Derived from Brown's (1978) foliage biomass equations and biomass-leaf area conversion factors from the indicated sources.

Species	Equation
Abies grandis (Dougl.) Lindl.[1]	$LA = 2.6195\ SA^{0.9562}(1.5916 + 0.2289\ SA^{0.5948})$
Larix occidentalis Nutt.[2]	$LA = \exp(-0.29223 + 1.0225\ \ln SA - 0.2451\ SA^{0.6092})$
Pinus contorta Dougl. ex Loud.[2]	$LA = 0.26253\ SA - 0.716$
Pinus ponderosa Dougl. ex Loud.[3]	$LA = (-1.3082 + 1.002\ \ln SA - 0.02211\ SA^{0.53046})$
Pseudotsuga menziesii (Mirb.) Franco[4]	$LA = 0.59325\ SA + 3.738$

[1]Gholz *et al.* (1976).
[2]R. H. Waring, unpub. data.
[3]Anderson *et al.* (1978).
[4]Smith (1980).

TABLE 2. Equations for estimating projected leaf area (LA) in square meters from DBH (D) in centimeters. Derived from Brown's (1978) foliage biomass equations and biomass-leaf area conversion factors from the indicated sources.

Species	Equation
Abies lasiocarpa (Hook.) Nutt.[1]	$LA = [0.00823\ D^2 - 9.407 + \ln(0.5966 - 0.01672\ D)]\ 6$
Picea engelmannii Parry ex Engelm.[1]	$LA = \exp[-1.3438 + 1.7096\ \ln D + \ln(0.5783 - 0.0128\ D)]\ 6$
Thuja plicata Donn[2]	$LA = \exp[-1.4368 + 1.6389\ \ln D + \ln(0.6174 - 0.00459\ D)]\ 8$
Tsuga heterophylla Raf. Sarg.[2]	$LA = \exp[-1.7002 + 1.7502\ \ln D + \ln(0.5474 - 0.01456\ D)]\ 8$

[1]Assumed to be similar to *Abies grandis*.
[2] Gholz *et al.* (1976).

calculated as the sum of canopy leaf area per hectare divided by 10,000 to provide units of leaf area, in square meters, per square meter of ground area.

Total cubic stemwood volume was estimated from diameter and height with volume tables compiled by Myers and Edminster (1972), Farr and LaBau (1971), and Faurot (1977). To estimate unknown tree heights, data from stands in which heights were measured over a range of diameters were fitted by least squares to the regression:

$$\ln (H/H^*) = b \ln (D/D^*) \qquad (2)$$

where H = height
D = DBH
H* = height of dominant trees
D* = DBH of dominant trees.

The coefficient, b, was estimated to be 0.63; the r^2 of the relationship is 0.99. Annual growth increments were estimated from current height, DBH, radial increment, and Daubenmire Habitat Type according to Stage's (1975) model.

The study area was stratified into three broad geographic zones recognized by Franklin and Dyrness (1973) (Fig. 1). After preliminary analysis, we subdivided their southern region (S) on the basis of forest types. In some places in this part of the state, the western hemlock (*Tsuga heterophylla*) zone west of the Cascades (west side) extends over the Cascade crest. The vegetation there is different from that occurring in the west-side western hemlock zone or in more typical east-side forests (Franklin and Dyrness 1973). Sample plots belonging to this forest type were identified by the presence of *Abies amabilis* (Dougl.) Forbes, *Abies procera* Rehd., *Pinus monticola*

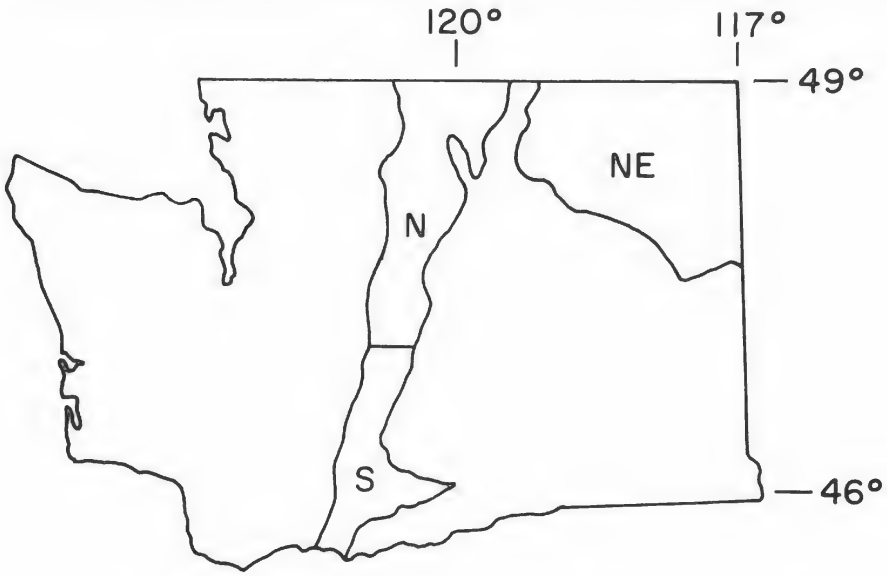


Figure 1. Geographic stratification of the study area into three broad vegetation zones. North (N), South (S), and Northeast (NE), based on Franklin and Dyrness (1973). The southern zone (S) was further subdivided into southwest (SW) and southeast (SE) vegetational zones which had irregular distributions within the broader zone but were easily distinguished on the basis of tree composition (see text for further explanation).

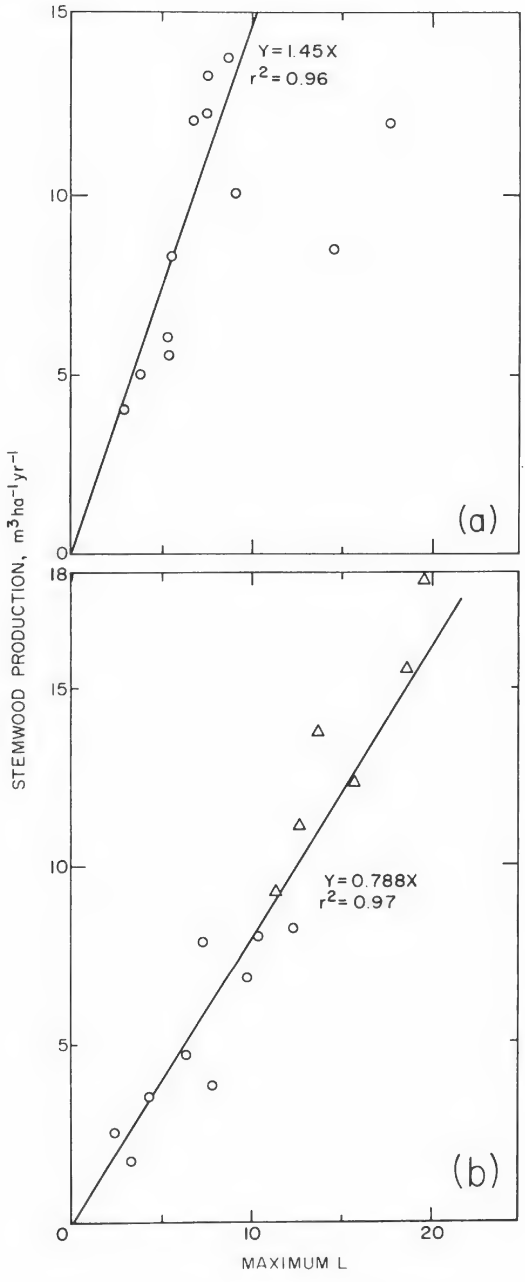


Figure 2. Relation of annual stemwood production to LAI for the study regions: (a) the NE and SE regions and (b) N and SW regions. Slopes of the regressions were significantly different, at the 5 percent level, for the two pooled data sets, a and b, up to an LAI of 10.

Dougl. ex D. Don, *Thuja plicata* Donn, or *Tsuga heterophylla* (Raf.) Sarg., and were grouped as the southern region, west-side type (SW); all other plots in this region were considered together as the east-side type (SE).

Results

The correlation between LAI and annual stemwood production calculated from average radial increment over the last five years was positive and significant at the five percent confidence level, but the relationship was not regionally independent (Fig. 2). Productivity increased in the NE and SE region at a rate of nearly 50 percent more than that observed for plots from N and SW regions, at least up to a LAI of 10. Two plots in the NE region fell below the linear predicted production. Both stands were of mixed composition and age with either a dense understory of slow growing *Abies grandis* and *Thuja plicata* or were over 225 years old. We suspect that natural or insect-induced mortality (Stoszek *et al.*, 1981) will soon occur and be followed by an increase in growth rate.

We correlated stemwood production with two other measures of productivity for a number of N and SW sites where Douglas-fir (*Pseudotsuga menziessi*) dominated fully stocked stands. First, site index alone was correlated with gross volume production; then a combination equation including site index, basal area, and age was used to predict yield after the procedures of Cochran (1979) (Fig. 3). Stemwood production was more closely related to LAI (Fig. 2b; $r^2 = 0.97$) than to either site index ($r^2 = 0.73$) or the combination equation ($r^2 = 0.91$).

From the field survey of variably stocked stands, sampling variation proved too great from only four to six points per stand to allow more than preliminary inferences

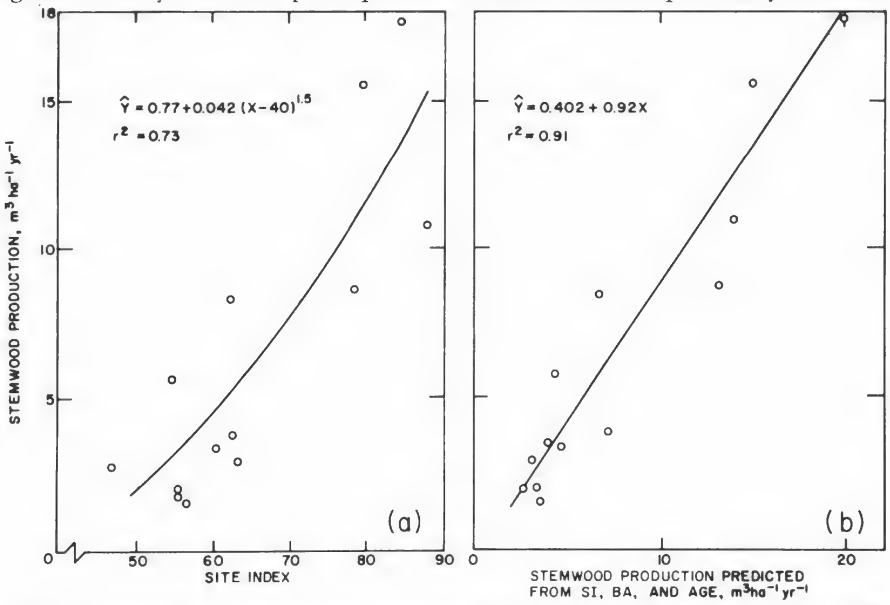

$\hat{Y} = 0.77 + 0.042\,(X-40)^{1.5}$
$r^2 = 0.73$
$\hat{Y} = 0.402 + 0.92X$
$r^2 = 0.91$
STEMWOOD PRODUCTION, $m^3 ha^{-1} yr^{-1}$
SITE INDEX
STEMWOOD PRODUCTION PREDICTED FROM SI, BA, AND AGE, $m^3 ha^{-1} yr^{-1}$
(a)
(b)

Figure 3. Relation of current stemwood production in 13 fully stocked stands in the N and SW regions to (a) site index and (b) productivity predicted by a combination equation including site index (SI), basal area (BA), and age.

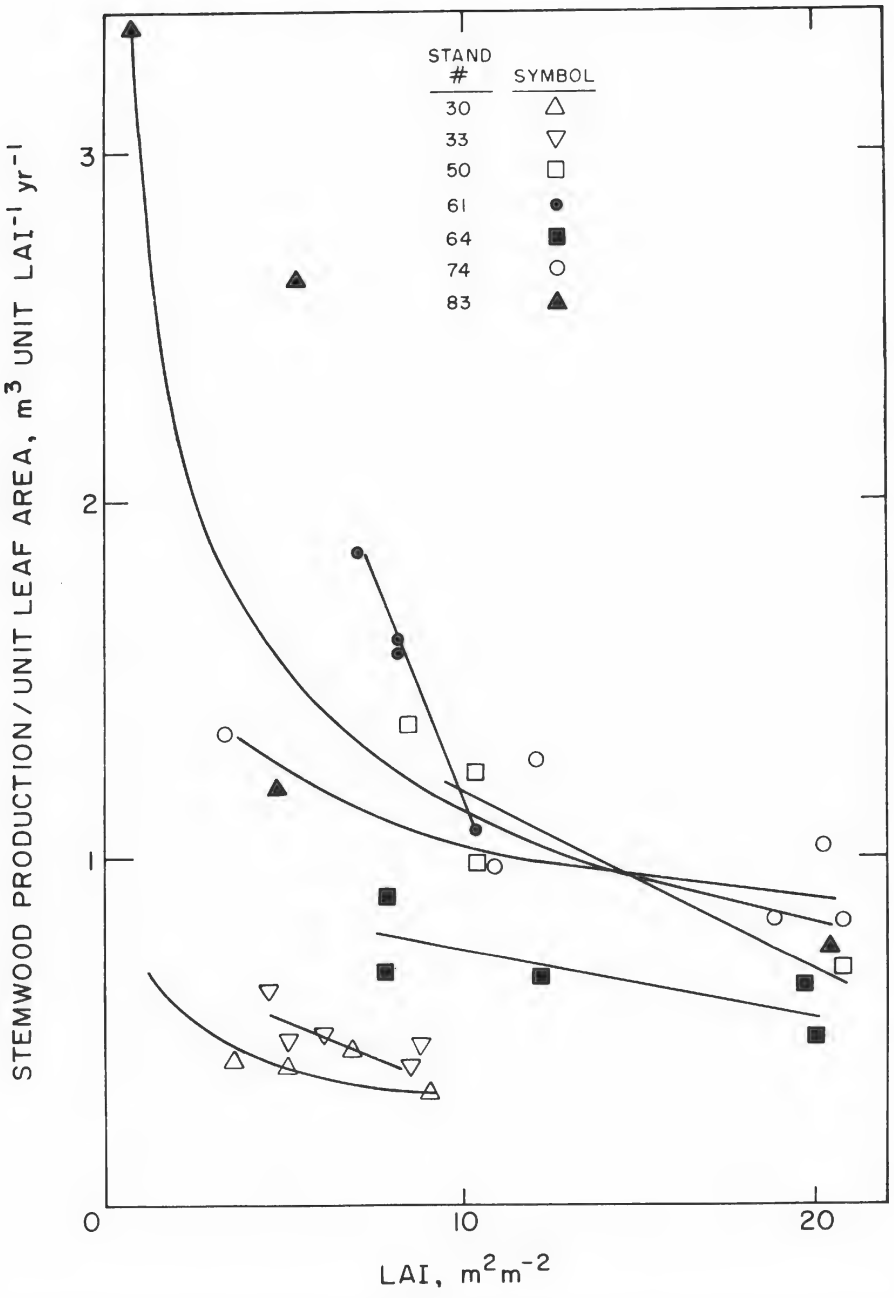


Figure 4. Relation of stemwood production per unit of leaf area to LAI. Lines represent data from seven distinct stands within which the stocking density of trees varied considerably.

about the relationship between estimated LAI and productivity on specific sites. In general, on a given site, net stemwood production per unit of leaf area decreased with increasing leaf area. In seven stands having a wide range in leaf area as a result of recent thinning, this relationship was significant at the 90 percent confidence level (Fig. 4). In undisturbed stands with high values of LAI, we noted that the crown on many trees became restricted to the upper bole. This constriction of the crown may promote more efficient capture of light and explain the small rate of decrease in growth efficiency at high leaf areas.

Discussion

More than two-fold differences in stemwood production by Douglas-fir stands with similar LAI have been reported previously (Waring *et al.*, 1980). Such differences have been attributed to climatic variables that influence net carbon uptake (Waring *et al.*, 1978). Another possibility is that total production may be similar, but that harsher edaphic environments stimulate a disproportionate allocation of carbohydrates into fine-root production (Keyes and Grier, 1981; Davidson, 1969). Because many trees are known not to produce annual growth rings under severe stress, wood production clearly is a relatively low priority compared with bud, shoot, and root growth (Gordon and Larson, 1968; Mooney, 1972; Rangnekar and Forward, 1973; Harris *et al.*, 1978). A real difference also may occur in net photosynthesis per unit of leaf area (Emmingham and Waring, 1977) or in respiration of various tissues. Any combination of these factors could interact to cause substantial differences in wood production for a given canopy leaf area.

Although changes in growth efficiency followed an expected relationship with LAI, the relationship was too asymptotic to project the maximum LAI at which growth would approach zero. At a given LAI, where data from a range of stands overlapped, we did find a proportionality between wood production per unit of leaf area and stand productivity. For example, at a stand LAI of approximately 8.0 (Fig. 4), wood production per unit of leaf area varied from 0.4 to 0.8 to 1.4, whereas the equivalent stand yields were 2.8, 8.7, and 18 $m^3ha^{-1}yr^{-1}$. No doubt additional characteristics of the canopy, such as live crown ratio and relative distribution of foliage with height, also are important. We recognize that trees differing in height but with similar leaf area have significantly different respiration and intercept light differently. Thus, net assimilation of wood per unit of leaf area should differ correspondingly.

In comparing regions, we found it essential to know tree height to estimate stemwood-volume growth accurately. Stemwood growth estimated from regression of stemwood biomass on DBH alone, although appropriate for local conditions, was lower than that estimated from DBH and height data combined.

The most important practical result of the study is the recognition that maximum canopy leaf area is a superior estimator to conventional forestry measures employed on pure even-aged stands. The lower the maximum LAI, the more valid this conclusion.

Acknowledgments

This research was supported by a grant from the USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. Colin MacLean, C. D. Bolsinger, and J. D.

Lloyd were especially helpful with preliminary planning for the field work and provided valuable advice throughout the course of the investigation.

Literature Cited

Albrektson, A., A. Aronson, and C. O. Tamm. 1977. The effect of forest fertilization on primary production and nutrient cycling in the forest ecosystems. Silva Fenn. 11:234-239.

Anderson, H. E., R. D. Schuette, and R. W. Mutch. 1978. Timelag and Equilibrium Moisture Content of Ponderosa Pine Needles. U.S. Dept. Agric., Forest Service, Res. Pap. INT-202, Ogden, Utah.

Baskerville, G. L. 1972. Use of logarithmic regressions in the estimation of plant biomass. Can. J. For. Res. 2:49-53.

Brown, J. K. 1978. Weight and Density of Crowns of Rocky Mountain Conifers. U.S. Dept. Agric., Forest Service, Res. Pap. INT-197, Ogden, Utah.

Cochran, P. H. 1979. Gross Yields for Even-aged Stands of Douglas-fir and White or Grand Fir East of the Cascades in Oregon and Washington. U.S. Dept. Agric., Forest Service, Res. Pap. PNW-263, Portland, Oregon.

Davidson, R. L. 1969. Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. Ann. Bot. 33:571-577.

Emmingham, W. H., and R. H. Waring. 1977. An index of photosynthesis for comparing forest sites in western Oregon. Can. J. For. Res. 7:165-174.

Farr, W. A., and V. J. LaBau. 1971. Volume Tables and Equations for Old-Growth Western Red Cedar and Alaska Cedar in Southeast Alaska. U.S. Dept. Agric., Forest Service, Res. Note PNW-167, Portland, Oregon.

Faurot, J. L. 1977. Estimating Merchantable Volume and Stem Residue in Four Timber Species: Ponderosa Pine, Lodgepole Pine, Western Larch, and Douglas-fir. U.S. Dept. Agric., Forest Service, Res. Pap. INT-196, Ogden, Utah.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. U.S. Dept. Agric., Forest Service, Gen. Tech. Rept. PNW-8, Portland, Oregon.

Gholz, H. L. 1979. Limits on Aboveground Net Primary Production, Leaf Area, and Biomass in Vegetational Zones of the Pacific Northwest. Oregon State Univ., Corvallis, Ph.D. thesis.

———, F. K. Fitz, and R. H. Waring. 1976. Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. Can. J. For. Res. 6:49-57.

Gordon, J. C., and P. R. Larson. 1968. Seasonal course of photosynthesis, respiration and distribution of ^{14}C in young *Pinus resinosa* trees as related to wood formation. Plant Physiol. 43: 1617-1624.

Hall, F. C. 1973. Plant Communities of the Blue Mountains in Eastern Oregon and Southeastern Washington. U.S. Dept. Agric., Forest Service, Pac. Northwest Reg. R6, Area Guide 3-1.

Harris, W. F., R. S. Kinerson, and N. T. Edwards. 1978. Comparison of belowground biomass of natural deciduous forests and loblolly pine plantations. Pedobiologia 17:369-381.

———, D. Santantonio, and D. McGinty. 1980. The dynamic belowground ecosystem, pp. 119-129 *in* R. H. Waring (ed.). Forests, Fresh Perspectives from Ecosystem Analysis. Proceedings 40th Annual Biology Coloquium. Oregon State Univ., Corvallis.

Keyes, M. R., and C. C. Grier. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11:599-605.

MacLean, C. D., and C. L. Bolsinger. 1973. Estimating Productivity on Sites with a Low Stocking Capacity. U.S. Dept. Agric., Forest Service, Res. Pap. PNW-152, Portland, Oregon.

Madgwick, H. A. I., and D. F. Olson. 1974. Leaf area index and volume growth in thinned stands of *Liriodendron tulipifera*. J. Appl. Ecol. 11:575-579.

Mooney, H. A. 1972. The carbon balance of plants. Annu. Rev. Ecol. & Systematics 3:315-345.

Myers, C. A., and C. B. Edminster. 1972. Volume Tables and Point Sampling Factors for Engelmann Spruce in Colorado and Wyoming. U.S. Dept. Agric., Forest Service, Res. Pap. RM-95, Ft. Collins, Colorado.

Rangnekar, O. V., and D. F. Forward. 1973. Foliar nutrition and wood growth in red pine: effects of darkening and defoliation on the distribution of ^{14}C-photosynthate in young trees. Can. J. Bot. 51:103-108.

Smith, R. H. 1980. Seasonal Variation in Leaf Weight and Nitrogen Content of Douglas-fir Plantations in the Coast Range and Cascade Mountains of Western Oregon. Oregon State Univ., Corvallis, M.S. thesis.

Stage, A. R. 1975. Prediction of Height Increment for Models of Forest Growth. U.S. Dept. Agric., Forest Service, Res. Pap. INT-164, Ogden, Utah.

Stoszek, K. J., P. G. Mika, J. A. Moore, and H. L. Osborne. 1981. Relationships of Douglas-fir tussock moth defoliation to site and stand characteristics in northern Idaho. For. Sci. 27: 431-448.

Waring, R. H., W. H. Emmingham, H. L. Gholz, and C. C. Grier. 1978. Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. For. Sci. 24:131-140.

———, K. Newman, and J. Bell. 1981. Efficiency of tree crowns and stemwood production at different canopy leaf densities. Forestry 54:15-23.
———, W. G. Thies, and D. Muscato. 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci. 26:112-117.
Wilkstrom, J. H., and S. B. Hutchinson. 1971. Stratification of Forest Land for Timber Management Planning on the Western National Forests. U.S. Dept. Agric., Forest Service, Res. Pap. INT-108, Ogden, Utah.

Received April 24, 1981
Accepted for publication December 4, 1981

Dirk Van Vuren[1]

Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331

and

Stephen E. Thompson, Jr.

Klah Klahnee Wildlife Sanctuary
P.O. Box 999
Sisters, Oregon 97759

Opportunistic Feeding by Coyotes

Abstract

Opportunistic feeding by coyotes (*Canis latrans*) was evaluated relating the diet of three coyotes during one year with regard to prey availability. Diet closely matched prey availability, supporting the description of the coyote as a highly flexible, opportunistic predator.

Introduction

Opportunistic predators select prey primarily on the basis of availability. The coyote is commonly regarded as an opportunistic predator; however, little is known about the relationship between the diet of individual coyotes and prey availability. Published studies of coyote diets were based on large or undetermined numbers of coyotes (Henderson, 1930; Murie, 1940; Sperry, 1941; Ferrel *et al.*, 1953; Korschgen, 1957), and hence reveal little about prey selection by individual coyotes. Furthermore, few authors related diets of coyotes to prey availability to show that coyotes do in fact eat whatever is available. Such studies related abundance of a single prey item to occurrence in coyote diets on an annual or seasonal basis (Fichter *et al.*, 1955; Tiemeier, 1955; Gier, 1957; Korschgen, 1957; Nellis and Keith, 1976; Johnson and Hansen, 1979). Availability of a diversity of prey species was not related to occurrence in coyote diets in a program of frequent, regular sample collection.

In this study, we related the diet of three coyotes during one year to availability of prey species; we evaluated prey selection by the smallest sample of coyotes possible. Opportunism would be indicated by a close relationship between diet and prey availability.

Methods

The 275 ha study area was located 9 km south of Sisters, Deschutes County, Oregon, on Klah Klahnee Wildlife Sanctuary and adjacent parts of Deschutes National Forest. Elevation was about 1100 m. Dominant vegetation was a ponderosa pine (*Pinus ponderosa*)-juniper (*Juniperus occidentalis*) forest. The shrub understory consisted of *Chrysothamnus nauseosus, C. viscidiflorus, Purshia tridentata, Arctostaphylos patula,*

[1]Present Address: 1147 Hilton Avenue, Napa, California 94558.

Ceanothus cordulatus, Ribes cereum, and *Artemisia tridentata.* About 40 ha were irrigated for pasture and alfalfa.

Three coyotes regularly foraged within the study area: an adult male, an adult female, and a yearling. During 700 hr of systematic observation in the study area, primarily from a 10 m tower, we regularly saw these three coyotes throughout the study. Other coyotes seldom used the area.

On 1 April 1976 we removed all coyote scats from 12 km of dirt roads located within and on the perimeter of the study area. On the first and fifteenth day of each month thereafter for one year, all coyote scats found on the 12 km route were collected. Each scat was washed in detergent soap and air dried. Contents were separated, and prey items were identified by comparison with a reference collection from the area. Percentage of scats in which prey items occurred was calculated on a monthly basis.

Heavy snowfall precluded scat collection on 1 December and 1 January. Scats deposited during each of these periods were included in two double collections, one from 16 November to 15 December, and the other from 16 December to 15 January. to obtain bimonthly estimates of coyote diets during this period, the number of scats in each double collection was halved, and each half was assigned the diet composition of the entire double collection.

Prey availability was determined by regular visual surveys of the study area within every bimonthly collection period. Surveys were conducted on foot and from a 10 m tower. We noted presence or absence of prey species and recorded events that appeared to cause noticeable changes in availability of certain prey species to coyotes.

Results and Discussion

A total of 308 scats was collected and analyzed. Coyotes used the study area consistently; more than one-half of the bimonthly samples contained 11 to 13 scats, and scats often were deposited regularly at certain points along the collection route.

Rabbits (primarily *Sylvilagus nuttalli*) and chipmunks (*Eutamias* spp.) were active throughout the year and appeared in coyote scats in all months (Fig. 1). Gophers (*Thomomys talpoides*) also were available all year and were eaten by coyotes during eight months.

Birds were always present and were recorded in scats throughout the year. In summer 1976, Brewer's Blackbirds (*Euphagus cyanocephalus*) were abundant ground nesters in the irrigated fields. The young of blackbirds and other ground nesting birds fledged primarily during July, which coincided with a high percentage of birds in coyote scats. Young of other species such as swallows (Hirundinidae) and bluebirds (*Sialia* spp.) fledged at this time and probably became more vulnerable to predation by coyotes.

Microtine rodents were present all year and were eaten by coyotes every month, except during winter. A peak in frequency of occurrence in scats during late summer paralleled the alfalfa harvest, which began in late July and continued until mid-October. The hay was mowed, raked, and baled; these activities increased the availability of microtines to coyotes by disturbing cover used by voles and by killing or injuring voles. Coyotes frequently were observed following the mower and catching or scavenging voles, or successfully hunting for them along newly raked windrows of hay.

Insects were always present in the study area and appeared in coyote scats during 10 months. Infrequent occurrence in scats during winter corresponded to the season

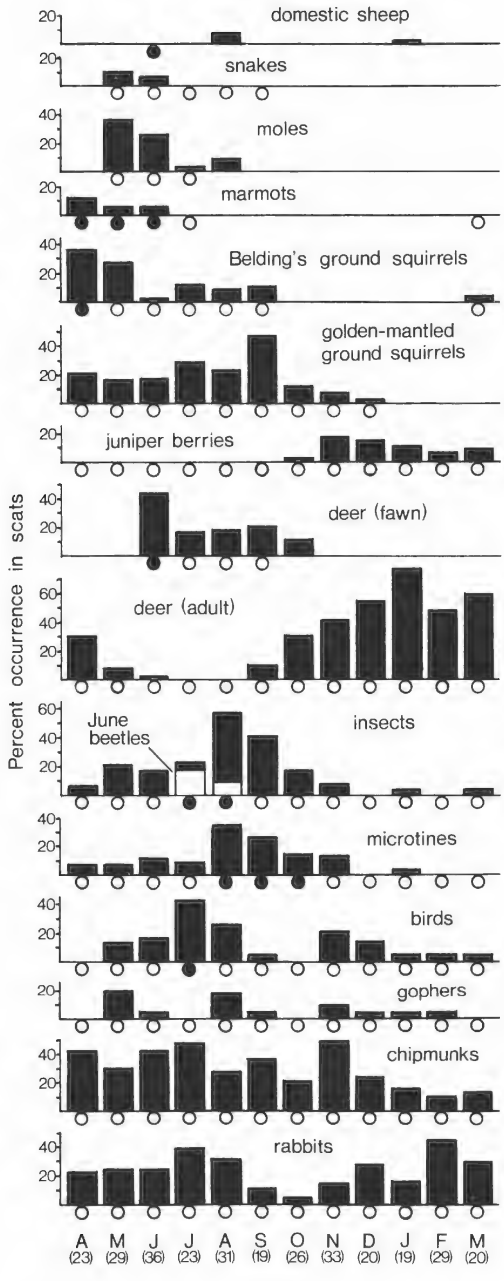


Figure 1. Percent occurrence of food items in coyote scats, at monthly intervals from April 1976 through March 1977, near Sisters, Oregon. Circles indicate those months when a prey species was present in the study area. Solid circles denote increased prey availability. The number of scats collected per month is shown in parentheses.

when insects were least active. June beetles (*Phyllophaga* spp.) appeared in large numbers on 18 July and were first recorded in scats in the next collection, on 1 August. Within three weeks the number of June beetles in the area declined abruptly, which coincided with their disappearance from coyote scats.

Adult mule deer (*Odocoileus hemionus*) were observed almost daily and were recorded in scats in every month except July and August. The abrupt increase in frequency of deer in scats during October coincided with the deer hunting season in Deschutes County; coyotes probably scavenged the remains of deer left by hunters. Adult deer were absent in coyote scats from 15 June to 1 September, when alternate prey species were most abundant and deer presumably were in good condition. Healthy deer are difficult to capture (Murie, 1940; Stebler, 1951; Ozoga and Harger, 1966).

Parturition of mule deer fawns occurred primarily during June (Paul Bonn, Oregon Department of Fish and Wildlife, pers. comm.) and coincided with the first appearance of fawns in coyote scats. Fawns were recorded in 44 percent of scats collected in June; Salwasser (1974) found high mortality in mule deer fawns during or shortly after parturition. Fawns appeared in seven of nine scat collections from 1 June to 15 October. Fawns began shedding their silky hair, which was important in identification of scats, during September (P. Bonn, pers. comm.), and we could not differentiate between fawns and adults after early October.

Juniper berries were available all year, but appeared in scats from 15 October to 1 April. Murie (1951) reported frequent winter use of juniper berries by coyotes in Arizona.

Golden-mantled ground squirrels (*Spermophilos lateralis*) first appeared from hibernation in early April but were not recorded in scats until the end of April, probably because the squirrels were relatively inactive shortly after emergence from hibernation. Golden-mantled ground squirrels were identified in 13 of 15 scat collections from late April until the onset of hibernation in late November and early December. Belding's ground squirrels (*S. beldingi*) emerged from hibernation in early March and were active until September; this period paralleled the occurrence of Belding's ground squirrels in coyote scats. The peak in occurrence of Belding's ground squirrels in scats in April coincided with the dispersal of yearling males of this species, which typically occurs soon after emergence from hibernation (Sherman, 1976).

Yellow-bellied marmots (*Marmota flaviventris*) emerged from hibernation in early March and were present through July. Thompson (1979) found that marmots in the study area were generally not vulnerable to coyote predation. However, marmot social structure changed in 1976, and from late April until the onset of hibernation many individuals dispersed from the colony. This period coincided with the occurrence of marmots in scats.

The coast mole (*Scapanus orarius*) was active almost exclusively below ground; although we found evidence of mole activity, we did not observe individuals during the study. Giger (1965) reported that juvenile coast moles in Tillamook County, Oregon, dispersed on the ground surface from May through July and were vulnerable to predation at that time; their occurrence in scats in this study paralleled their presumed above-ground presence.

Garter snakes (*Thamnophis sirtalis*), the only snakes in the area, were first observed on 15 May and were seen frequently thereafter through the summer. The initial

appearance in the study area matched the first occurrence in coyote scats in the 15 May collection. Snakes were found in scats in the next three collections but were absent in all other collections, despite the continued presence of snakes in the study area.

A herd of 2400 domestic sheep was in and adjacent to the study area during the last week of June, yet sheep did not appear in scats during June or July. Sheep were found in three scats, in August and January. The absence of sheep in coyote scats possibly was due to the active herding by a man and two dogs, the availability of many alternative prey species, or a lack of previous experience with sheep. This herd was the first to pass near the area in over eight years.

The occurrence of prey items in the diet of three coyotes closely paralleled the presence of these prey in the study area. The coyotes ate most prey species whenever the prey were present and responded immediately to a newly available prey item by including it in their diet. The results of this study provide evidence that the coyote is a highly flexible, opportunistic predator. These attributes account, in part, for the continued success of the coyote as a species.

Acknowledgments

Klah Klahnee Wildlife Sanctuary funded this study. We thank Brett Adams for assistance in collecting and washing scats. B. E. Coblentz, J. A. Crawford, and D. S. deCalesta provided helpful criticism of the manuscript. This is Klah Klahnee Wildlife Sanctuary Contribution No. 1.

Literature Cited

Ferrel, C. M., H. R. Leach, and D. F. Tillotson. 1953. Food habits of the coyote in California. Calif. Fish and Game 39: 301-341.

Fichter, E., G. Schildman, and J. H. Sather. 1955. Some feeding patterns of coyotes in Nebraska. Ecol. Monogr. 25:1-37.

Gier, H. T. 1957. Coyotes in Kansas. Kansas Agric. Exp. Stn. Bull. 393.

Giger, R. D. 1965. Surface activity of moles as indicated by remains in Barn Owl pellets. Murrelet 46:32-36.

Henderson, W. C. 1930. The control of the coyote. J. Mammal. 11:336-353.

Johnson, M. K., and R. M. Hansen. 1979. Coyote food habits on the Idaho National Engineering Laboratory. J. Wildl. Manage. 43:951-956.

Korschgen, L. J. 1957. Food habits of the coyote in Missouri. J. Wildl. Manage. 21:424-435.

Murie, A. 1940. Ecology of the Coyote in the Yellowstone. Fauna of the Natl. Parks of the U.S., Fauna Ser. 4.

———. 1951. Coyote food habits on a southwestern cattle range. J. Mammal. 32:291-295.

Nellis, C. H., and L. B. Keith. 1976. Population dynamics of coyotes in central Alberta, 1964-1968. J. Wildl. Manage. 30:389-399.

Ozoga, J. J., and E. M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. J. Wildl. Manage. 30:809-818.

Salwasser, H. 1974. Coyote scats as an indicator of time of fawn mortality in the North Kings deer herd. Calif. Fish and Game 60: 84-87.

Sherman, P. W. 1976. Natural Selection among Some Group-living Organisms. Univ. Michigan, Ann Arbor. Ph.D. thesis.

Sperry, C. C. 1941. Food Habits of the Coyote. U.S. Fish and Wildl. Serv. Res. Bull. 4.

Stebler, A. M. 1951. The Ecology of Michigan Coyotes and Wolves. Univ. Michigan, Ann Arbor. Ph.D. thesis.

Thompson, S. E., Jr. 1979. Socioecology of the Yellow-bellied Marmot in Central Oregon. Univ. Calif., Berkeley. Ph.D. thesis.

Tiemeier, O. W. 1955. Winter foods of Kansas coyotes. Trans. Kansas Acad. Sci. 58:196-207.

Received May 26, 1980
Accepted for publication September 2, 1980

Marion Bacon[1]

Eastern Washington University
Cheney, Washington 99004

A Study of Surface Waters and Sediments in Southern Spokane County, Washington, for the Presence of *Yersinia enterocolitica*

Abstract

During the period September 1977 through May 1979, investigations were conducted for the presence of the pathogenic bacterium, *Yersinia enterocolitica*, in surface waters of southern Spokane County, Washington. Collection sites were located on the Spokane River and at various lakes, ponds, marshes, and streams. Only one of 433 water and sediment samples was positive for *Y. enterocolitica*.

During the period September 1977 through May 1979, investigations were conducted at Eastern Washington University, Cheney, Washington, for the presence of the pathogenic bacterium, *Yersinia enterocolitica* (Frederiksen, 1964), in surface waters of southern Spokane County.

Methods and materials employed for isolating the bacterium included those used by Harvey *et al.* (1976), Saari and Quan (1976), and Wetzler (1978-1979). All of these prescribe incubation in enrichment media of inocula taken directly from water samples and the subsequent plating out of these cultures onto diagnostic agars. During most of the present studies, a modification was made of these methods in that bacteria in the water samples were concentrated by passing 50-500 ml of sample through a cellulose filter, pore size 0.45μ (Millipore). The entire filter disk was then used to inoculate a culture tube of enrichment broth.

Water and/or sediment samples were taken at 30 different sites at various lakes, ponds, marshes, minor streams, and the Spokane River. The most numerous collections were made from nine sites on the Spokane River along its course through metropolitan Spokane, and from the Turnbull Refuge Natural Area.

Only one of a total of 433 water and sediment samples was positive for *Y. enterocolitica.* This sample was from the Spokane River within the city limits. Samples taken from this site on 26 other occasions all tested negative.

The almost entirely negative results in this study may have been due in part to the fact that no completely reliable method has yet been developed for isolating *Y. enterocolitica* when the organism is present in low concentration, especially when such competing organisms as *Proteus* spp. are present. However, the procedures used in the present study were all adaptations of those by which other investigators have successfully isolated *Y. enterocolitica* from water in California (Harvey *et al.*, 1976), Colorado (Saari and Quan, 1976), and western Washington (Prior, 1976; Wetzler, 1978). The inference, therefore, from the results of the present study is that there is a very low incidence of *Y. enterocolitica* in the surface waters of southern Spokane Couny.

---

[1]Present address: 107 Seventh Street, Cheney, Washington 99004.

Acknowledgments

This project was supported principally by research funds provided by Eastern Washington University. Jimmie A. Lakey completed studies involving collections from the Spokane River from June to November 1978 as the basis of a research report in partial fulfillment of the requirements for the degree of Master of Science in Biology. Field and laboratory work were conducted with the assistance of graduate student Jimmie A. Lakey, and undergraduates George F. Hodges, Randolph E. Noltre, Keven L. Llewellyn, William P. Werschler, Brad D. Bisson, and Raymond M. Tsuchida, all of Eastern Washington University.

Dr. Ted F. Wetzler, University of Washington, provided valuable advice on selection of materials and methods, and verified the author's identification of the isolate of *Y. enterocolitica.*

Literature Cited

Harvey, S., J. R. Greenwood, M. J. Pickett, and R. A. Mah. 1976. *Yersinia enterocolitica* from streams and lakes of California. Appl. Environ. Microbiol. 32:352-354.

Prior, B. W. H. 1976. *Yersinia enterocolitica* in Surface Waters of Western Washington. Univ. of Washington, Seattle. M.A. thesis (Thesis No. WA 724373).

Saari, T., and T. J. Quan. 1976. Waterborne *Yersinia enterocolitica* in Colorado. Presented at the Annual Meeting of Amer. Soc. Microbio., Atlantic City. (Abstr. No. C119.)

Wetzler, T. F. 1978. Univ. of Washingon, Seattle. Pers. comm.

———. 1979. Univ. of Washington, Seattle. Pers. comm.

Received June 20, 1980
Accepted for publication September 15, 1980

Daniel W. Uresk

Rocky Mountain Forest and Range Experiment Station
South Dakota School of Mines Campus
Rapid City, South Dakota 57701

and

Virginia A. Uresk[1]

Rockwell Hanford Operations
Environmental Engineering Section
Richland, Washington 99352

Diets and Habitats of Mule Deer in South-central Washington

Abstract

Forty-four food items were identified in the fecal pellets of the mule deer (*Odocoileus hemionus hemionus*) on three areas of the Hanford Site in south-central Washington. Microscopic analysis of plant fragments indicated that bitterbrush (*Purshia tridentata*) was the most common species occurring in the diets of deer from the B-C Cribs area. Russian thistle (*Salsola kali*) and goldenrod (*Solidago* sp.) were the most abundant plants found in the fecal pellets collected from B Pond and Gable Mountain Pond habitats, respectively. The similarity in diets among the habitats was low, ranging from 10 to 16 percent. Preference indices of forage plants among sites were not similar (7 to 19 percent), indicating that deer are selecting different food plants at each site, even though many plants are common to all three sites. Twelve species were sampled for canopy cover and frequency of occurrence in the B-C Cribs and B Pond areas; 22 species were identified on the Gable Mountain site. The most commonly occurring plant was cheatgrass (*Bromus tectorum*) in all three sites. The similarity in frequency and canopy cover of plants was low among sites, indicating that each site is different when these two parameters are considered.

Introduction

On rangelands, knowledge of the availability of forage plants and the diets of herbivores aids in formulating better management programs for both plants and animals. The diets of mule deer (*Odocoileus hemionus hemionus*), a common herbivore on shrub-steppe rangeland of south-central Washington, have been studied by microhistological examination of fecal pellets. Elsewhere, food habits of the mule deer in eastern Oregon on bunchgrass rangeland have been reported by Edgerton and Smith (1971). Other studies of food habits of mule deer in bunchgrass rangelands have been reported by Nellis and Ross (1969), Lovaas (1958), Morris and Schwartz (1957), and Wilkins (1957).

The purpose of this investigation was to study the dietary habits of mule deer at three locations on the Hanford Site, a large nuclear facility, in south-central Washington (Fig. 1). The study area has not been grazed by livestock since 1943, but small mammals such as the black-tailed hare (*Lepus californicus*) and Townsend ground squirrel (*Spermophilus townsendii*) also reside there.

Study Area and Methods

The study area is located on the Department of Energy's (DOE) Hanford Site in south-

[1]Present address: 4406 Ridgewood, Rapid City, South Dakota 57701.

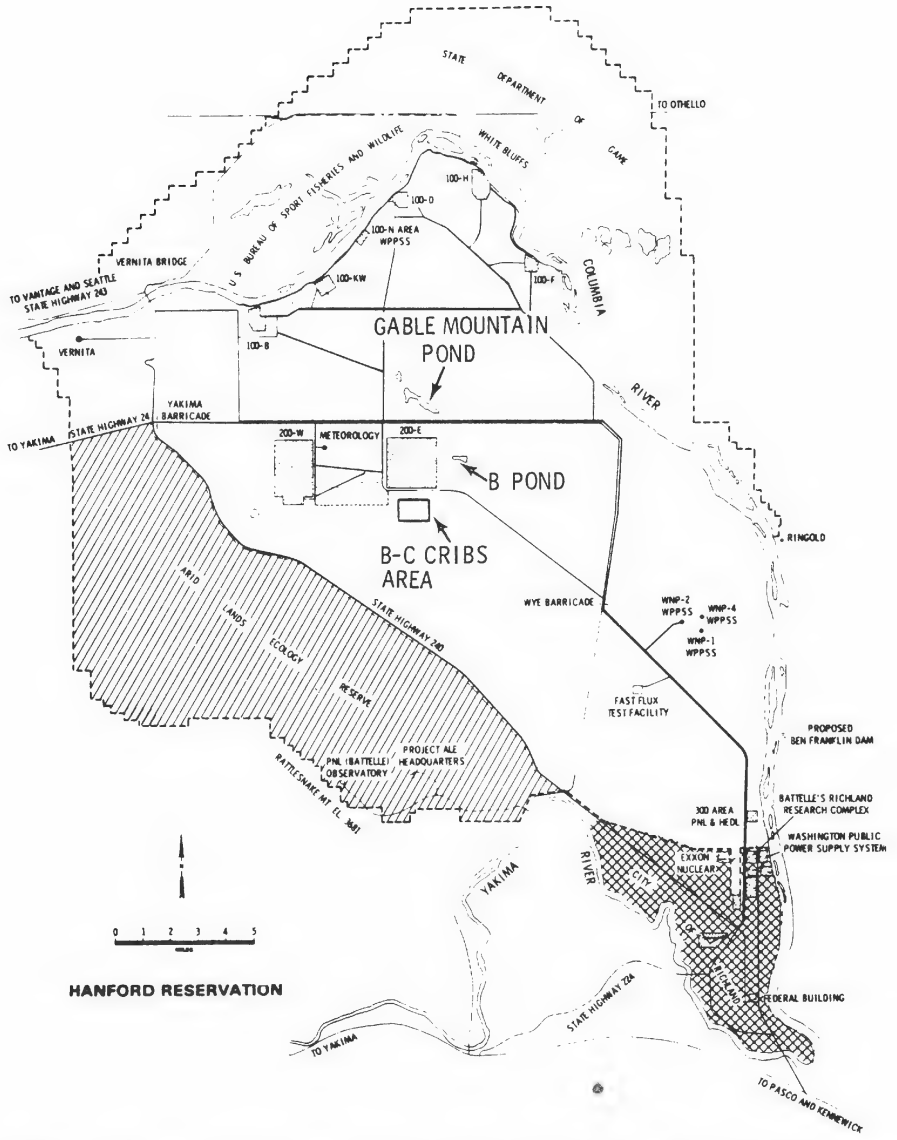


Figure 1. Study areas (Gable Mountain Pond, B. Pond, and B-C Cribs Area) on the Hanford Site in south-central Washington.

central Washington on a large plain which slopes gently toward the Columbia River. The elevation is approximately 223 m, and the area has an average annual rainfall of 16 cm. The soils are primarily Rupert sands and Burbank loamy sand (Hajek, 1966). The topography is described as gently undulating. The area's vegetation is described as an *Artemesia tridentata/Poa sandbergii* association (Daubenmire, 1970). The native

vegetation has been extensively invaded by alien annuals, especially cheatgrass, which is the dominant understory species (Cline *et al.*, 1977).

Three study sites were selected as representative of distinctive habitats. One site (Gable Mountain Pond) is located near a 29 ha man-made pond with dense riparian vegetation (Fig. 1). The second study site (B Pond) is near an 18 ha man-made pond with sparse riparian vegetation. The third site (B-C Cribs) is located in the sagebrush/bluegrass association. All three sites are near chemical separation and waste management operations associated with DOE's plutonium processing facilities.

Vegetation was analyzed for species composition, canopy cover by plant species, and frequency of occurrence. Four transects, adjacent and parallel to the shoreline of the ponds, were examined at each site. Transects sampled by Cline *et al.* (1977) in the B-C Cribs area were also used in this study. Ocular estimates of canopy cover and frequency of occurrence were made on 50 plots, each 2 x 5 dm, 0.1 m^2, systematically spaced at 1-m intervals along each 50-m line transect (Daubenmire, 1959). Canopy cover and frequency of occurrence values were summarized for each line transect. All vegetation data were collected in May 1977.

Deer fecal pellets were collected along repeated transects located randomly within the study site. At Gable Mountain Pond and B Pond, four transects were located adjacent and parallel to the shoreline of the ponds. The first 10 pellet groupings (new and old) encountered along the transect were collected and individually placed in paper bags for dietary analysis. Forty pellet groups were collected at each of the pond sites. At the B-C Cribs site, two transects were randomly located within the radiation control area, and the first 10 pellet groups encountered on each transect were collected for dietary analysis. A total of 100 pellet groups was collected from all three study sites. The pellets were dried at 70°C for 48 hours and ground in a Wiley mill (1 mm screen) to homogenize the sample. All fecal pellet groups, both new and old, were collected in late summer 1976 and included pellets from all seasons. Pellets dating over a 10-year period may persist on this study area (Uresk, 1978).

Five slides were prepared for each pellet group after the ground sample was washed over a 0.1 mm screen (Sparks and Malechek, 1968). The slides were prepared with Hertwig's solution and Hoyer's solution and dried for approximately 72 hr at 60°C (Baumgartner and Martin, 1939).

The slides were examined microscopically to identify plant fragments, using epidermal cell characteristics. Identifications were confirmed as necessary by comparing them to reference slides prepared from plant specimens identified and collected from the study area. Twenty microscope fields were examined on each slide. All identifiable fragments were recorded, as were the unknowns. Plant nomenclature follows Hitchcock and Cronquist (1973).

Statistical analyses follow Snedecor and Cochran (1967). Kulczynski's similarity indices (Oosting, 1956) and Spearman's rank correlation coefficients (r_s) (Siegel, 1956) were calculated for diet and plant communities to measure the degree of association.

Preference indices were calculated by dividing the relative frequency of a plant species in the diet by the relative frequency in the habitat. When a plant did not occur in the habitat, a value of 0.1 was used as the divisor. All values were rounded to the nearest one-tenth unit. Preference indices as used here are regarded only as a guide to food

preferences rather than as absolute values. Other preference indices are presented by Krueger (1972).

Results

Characterization of Vegetation

Table 1 presents the frequency of occurrence and canopy cover of plants at the three study sites. A total of 12 species was sampled in the B-C Cribs and B Pond areas; 22 species were present on the Gable Mountain site. The most common (abundant) plant at all three sites was cheatgrass. Tansy mustard (*Descurainea pinnata*) and Russian thistle were the most common forbs present at the B-C Cribs and B Pond areas, respectively. Matted cryptantha (*Cryptantha circumscissa*) was the most common forb at the Gable Mountain Pond study area. Big sagebrush (*Artemisia tridentata*) was abundant in the B-C Cribs and B Pond areas, and hopsage (*Atriplex spinosa*) was the dominant shrub at the Gable Mountain Pond area.

TABLE 1. Frequency of occurrence (percent) and canopy cover (percent) within three habitat sites used by mule deer on the Hanford Site.

	Frequency of Occurrence[1]			Canopy Cover[1]		
	B-C Cribs $\bar{X}\pm SE$	B Pond $\bar{X}\pm SE$	Gable Pond $\bar{X}\pm SE$	B-C Cribs $\bar{X}\pm SE$	B Pond $\bar{X}\pm SE$	Gable Pond $\bar{X}\pm SE$
Grasses and Grass-like Plants						
Cheatgrass (**Bromus tectorum**)	51.0± 6.3	48.0±16.9	46.5±17.6	2.4± 0.7	5.7± 3.3	12.3± 8.8
Sandberg bluegrass (**Poa sandbergii**)	17.0± 5.1	25.0±21.8	18.5±17.8	3.4± 1.7	8.0± 7.2	3.5± 3.4
Sixweek fescue (**Festuca octoflora**)	6.5± 2.5	3.0± 1.9	4.0± 2.8	0.2± 0.1	<0.1	0.1± 0.1
Three-square bullrush (**Scirpus americanus**)			1.5± 1.5			0.1± 0.1
Bigstem bullrush (**Scirpus** sp.)			2.5± 2.5			0.6± 0.6
Little stem bullrush (**Scirpus** sp.)			1.5± 1.5			0.1± 0.1
Total				6.0	13.7	16.7
Forbs						
Tansy mustard (**Descurainia pinnata**)	11.0± 0.6	3.5± 2.9	7.5± 7.5	0.4± 0.1	<0.1	0.3± 0.3
Ragweed (**Ambrosia acanthicarpa**)	2.5± 1.5		5.5± 5.5	0.6± 0.5		0.1± 0.1
Slimleaf goosefoot (**Chenopodium leptophyllum**)	0.5± 0.5			0.1± 0.1		
Wing-nut cryptantha (**Cryptantha pterocarya**)	0.5± 0.5			<0.1		
Russian thistle (**Salsola kali**)		47.0±26.6	14.0± 8.4		3.1± 1.9	0.7± 0.4
Jim Hill mustard (**Sisymbrium altissimum**)		21.0±15.2	10.0± 6.6		1.5± 1.4	0.7± 0.5
Buckwheat (**Eriogonum** spp.)	2.0± 1.1	17.5±11.4	6.5± 6.5	<0.1	1.2± 0.8	0.4± 0.4
Matted cryptantha (**Cryptantha circumscissa**)	10.0± 3.6	2.5± 1.9	30.0±23.5	0.4± 0.2	<0.1	7.5± 7.1
Threadleaf phacelia (**Phacelia linearis**)		1.0± 1.0	0		<0.1	
Common mullen (**Verbascum thapsus**)		2.0± 2.0	0		2.5± 2.5	

TABLE 1 (Continued)

Pale comandra (**Comandra pallida**)	3.5± 2.4			0.4± 0.3		
Wild lettuce (**Lactuca serriola**)			1.0± 1.0			<0.1
Draba (**Draba verna**)			4.5± 4.5			0.2± 0.2
Goatbeard (**Tragopogon dubius**)			0.5± 0.5			<0.1
Astragalus (**Astragalus** spp.)			4.0 ±2.4			0.2± 0.2
Yarrow (**Achillea millefolium**)			0.5± 0.5			<0.1
Fiddleneck (**Amsinckia lycopsoides**)			0.5± 0.5			<0.1
Wallflower (**Erysimum asperum**)			1.5± 1.5			0.1± 0.1
Total				1.9	8.3	10.2
Shrubs						
Big sagebrush (**Artemisia tridentata**)	21.5± 4.0	8.5± 7.8	3.5± 3.5	16.5± 4.4	6.8± 6.1	2.1± 2.1
Green rabbitbrush (**Chrysothamnus viscidiflorus**)	2.0± 1.4			0.7± 0.5		
Hopsage (**Atriplex spinosa**)		1.5± 1.5	4.5± 4.5		0.9± 0.9	2.7± 2.7
Willow (**Salix** spp.)			1.5± 1.5			0.5± 05.
Total				17.2	7.7	5.3
Others						
Total	97.0± 1.7	99.0± 1.0	100.0± 0.0	59.1± 7.7	41.6±16.8	54.3± 8.3
Total (dead)	97.0± 1.3	47.0±27.2	49.0±28.3	53.4± 6.6	21.3±12.9	28.2±16.4
Cheatgrass (dead)		47.0±27.2	24.5±24.5		20.4±12.5	13.9±13.9
Sagebrush (dead)	4.5± 2.1			3.0± 1.4		
Unknown forbs		0.5± 0.5	0.5± 0.5		<0.1	<0.1

[1]Sample size, N=4 transects.

Grasses and grass-like plants provided 17, 14, and 6 percent of the canopy cover on the Gable Mountain Pond, B Pond, and B-C Cribs study areas, respectively (Table 1). Forbs contributed less canopy cover than the grasses and grass-like plants. Gable Mountain study area had the largest forb canopy cover, 10 percent. Forbs provided only 2 percent of the cover at the B-C Cribs area.

Shrubs dominated the three study areas, with the highest canopy cover occurring on the B-C Cribs site (17 percent) and the least at Gable Mountain Pond (5 percent). Sagebrush and hopsage were the major shrubs present on these areas. Canopy cover averaged 52 percent in the three areas; bare ground averaged approximately 48 percent.

Deer Diets

Forty-four plants were identified in the fecal pellets of deer collected from the three areas (Table 2). Frequency of occurrence values show that bitterbrush was eaten more often than any other species by deer in the B-C Cribs area. Bitterbrush did not occur in the vegetation plots, but is present in the study area. Russian thistle comprised 76 percent and goldenrod 40 percent of the diets of deer from B Pond and Gable Mountain Pond, respectively. Forbs provided the mainstay of the mule deer diet and were found more frequently in pellets from Gable Mountain and B Ponds than in pellets from the B-C Cribs site, in which shrubs appeared most often. Shrubs were secondary in

importance at the B Pond and Gable Mountain sites, with the grasses and grass-like plants being least frequent in mule deer diets. The average dietary composition based upon relative frequency at all sites consisted of 2 percent grasses, 43 percent shrubs, and 52 percent forbs.

Relative preference values are shown in Table 3. These indices are based on relative

TABLE 2. Botanical composition (percent frequency of occurrence) of fecal pellets collected from mule deer on three habitat sites on the Hanford Site.

	B-C Crib[1] $\bar{X}$±SE	B Pond[2] $\bar{X}$±SE	Gable Pond[2] $\bar{X}$±SE
Grasses and Grass-like Plants			
Needle-and-thread (**Stipa comata**)	<0.5		
Sandberg bluegrass (**Poa sandbergii**)	<0.5	0.6±0.3	<0.5
Bluebunch wheatgrass (**Agropyron spicatum**)			<0.5
Canary grass (**Phalaris arundinacea**)			0.6±0.6
Three-awn (**Aristida** sp.)			<0.5
Cheatgrass (**Bromus tectorum**)	<0.5	1.7±0.6	3.4±1.1
Carex (**Carex** spp.)		<0.5	<0.5
Horsetail (**Equisetum** sp.)		<0.5	2.1±1.1
Barnyard grass (**Echinochloa crusgalli**)		6.8±1.3	
Muhly grass (**Muhlenbergia** sp.)			<0.5
Indian ricegrass (**Oryzopsis hymenoides**)			<0.5
Old witchgrass (**Panicum** sp.)		<0.5	<0.5
Cattail (**Typha latifolia**)			<0.5
Sand dropseed (**Sporobolus cryptandrus**)		<0.5	
Forbs			
Astragalus (**Astragalus** spp.)	<0.5	<0.5	1.9±1.7
Bassia (**Bassia hyssopifolia**)			4.4±1.6
Tansy mustard (**Descurainia pinnata**)		<0.5	
Wild lettuce (**Lactuca serriola**)			1.9±0.7
Bladderpod (**Lesquerella** sp.)			<0.5
Lupine (**Lupinus** spp.)		<0.5	<0.5
White sweet clover (**Melilotus alba**)	3.5±2.2[3]		23.2±3.9
Microsteris (**Microsteris** spp.)		<0.5	
Evening primrose (**Oenothera** spp.)	8.7±3.5	0.9±0.7	<0.5
Phlox (**Phlox longifolia**)			<0.5
Prickly pear (**Opuntia polyacantha**)		<0.5	
Indian wheat (**Plantago purshii**)			<0.5
Willow-weed (**Epilobium paniculatum**)		<0.5	<0.5
Russian thistle (**Salsola kali**)	2.9±0.7	75.5±4.0	5.2±2.2
Jim Hill mustard (**Sisymbrium altissimum**)			<0.5
Goldenrod (**Solidago** sp.)	1.4±0.4[3]	6.1±1.9	39.7±5.4
Globe mallow (**Sphaeralcea munroana**)	<0.5	10.9±4.4	1.8±1.0
Buttercup (**Ranunculus** sp.)			<0.5
Common mullen (**Verbascum thapsus**)	<0.5[3]	1.9±1.9	
Shrubs			
Big sagebrush (**Artemisia tridentata**)			<0.5
Bitterbrush (**Purshia tridentata**)	79.4±7.3		2.2±2.2
Grey rabbitbrush (**Chrysothamus nauseosus**)		<0.5	<0.5
Hopsage (**Atriplex spinosa**)			<0.5
Willow (**Salix** spp.)	18.1±5.8[3]	8.3±2.8	32.3±5.3
Trees			
Russian olive (**Elaeagnus angustifolia**)		10.9±4.4	
Others			
Moss			<0.5
Seeds	1.2±1.2	4.5±1.6	1.6±0.6
Unknown forbs			<0.5
Unknown grass		<0.5	<0.5
Unknown sedge		<0.5	<0.5

[1]Sample size, N=20 pellet groups.

[2]Sample size, N=40 pellet groups.

[3]These plants are not expected to occur in the B-C Cribs area, which indicate deer would move into this area primarily from B Pond site.

TABLE 3. Preference indices of mule deer by food items on three areas of the Hanford Site.

	B-C Cribs	B Pond	Gable Mtn. Pond
Grasses and Grass-likes			
Needle-and-thread	<1		
Sandberg bluegrass	<1	<1	<1
Bluebunch wheatgrass			2
Canary grass			6
Three-awn			<1
Cheatgrass	<1	<1	<1
Carex		2	3
Horse-tail		1	2
Barnyard grass		68	
Muhly grass			<1
Indian ricegrass			1
Old witchgrass		<1	<1
Cattail			<1
Sand dropseed		<1	
Forbs			
Astragalus	1	<1	19
Bassia			44
Tansy mustard		<1	
Wild lettuce			3
Bladderpod			<1
Lupine species		<1	<1
White sweet clover	35[1]		232
Microsteris		<1	
Evening primrose	87	9	2
Phlox			3
Prickly pear		<1	
Indianwheat			1
Willow-weed		2	<1
Russian thistle	29	3	1
Jim Hill mustard			<1
Goldenrod	14[1]	61	397
Globe mallow	1	109	18
Buttercup			3
Common mullen	1[1]	2	
Shrubs			
Big sagebrush			<1
Bitterbrush	794		22
Grey rabbitbrush			<1
Hopsage			<1
Willow	181[1]	83	323
Trees			
Russian olive		109	
Others			
Moss			<1
Seeds	9[1]	45	16

[1]These plants are not expected to occur in the B-C Cribs area, which indicates deer would move into this area from B Pond Site.

frequency values for plants occurring in the diets and in each of the study areas. When a plant species is scarce in the field but is found frequently in the fecal pellets of deer, it is assumed that this particular plant is being actively selected by the foraging animal. Generally, seven species of plants were preferred in each study area. Bitterbrush was the preferred species in the B-C Cribs area; both globe mallow (*Sphaeralcea munroana*) and Russian olive (*Eleagnus angustifolia*) were preferred in the B Pond area. Goldenrod was the preferred forage plant in the Gable Mountain Pond area. Cheatgrass was abundant in all areas but was not a preferred food item. However, Russian thistle was abundant in the deer diet and was sought by the deer foraging in the B-C Cribs sites.

Similarity indices and rank-order correlation coefficients comparing dietary and habitat analyses of the three areas are presented in Table 4. Similarity indices show the similarity between categories occurring at the study sites, while rank-order correlation coefficients show relationships among the categories when the sites are compared. A strong relationship was evident in diets of deer between the B-C Cribs and Gable Mountain areas, as shown by a significant rank order correlation coefficient. Preference indices of forage plants consumed by deer showed low similarity indices when the three sites were compared, demonstrating that forage plants highly preferred at one site may not be sought at another site.

TABLE 4. Average similarity indices (percent) and rank-order correlation coefficents (r_s) of mule deer diets, preference indices, frequency of occurrence and canopy cover when the three areas are compared.

Category	B-C Cribs versus B Pond			B-C Cribs versus Gable Pond			B Pond versus Gable Pond		
	n	%±SE	r_s	n	%±SE	r_s	n	%±SE	r_s
Deer diets	27	10±4	+0.28	38	10±4	+0.54[1]	43	16±4	+0.05
Forage preference	27	12±4	+0.17	38	7±3	+0.40[2]	43	19±5	+0.01
Frequency of occurrence	22	26±8	+0.34	31	23±6	+0.40[2]	28	35±8	+0.67[1]
Canopy cover	22	22±6	+0.18	31	18±6	+0.26	28	31±7	+0.67[1]

[1]Significant at $\alpha \leq 0.01$.

[2]Significant at $\alpha \leq 0.05$.

Similarity indices comparing frequency of occurrence of plants in the habitats among the sites were low, ranging from 23 to 28 percent. Significant rank-order correlations did occur when comparisons among B-C Cribs versus Gable Mountain Pond and B Pond versus Gable Mountain Pond were evaluated. These correlations show that these habitats were related in plant species frequency. Canopy cover by plant species did not show any high similarity indices; however, a significant correlation did occur between B Pond and Gable Mountain Pond habitats.

Discussion

In the arid region of south-central Washington at the Hanford Site, mule deer are found primarily in riparian habitats along the Columbia River (Hedlund, 1975). Mule deer are also commonly found at Hanford, near man-made ponds which contain effluent from nuclear waste operations. These ponds provide a source of water, food, and cover and are important in arid regions in supporting wildlife. The Hanford Site supports a sizable herd of mule deer that has been protected from hunting since 1943.

Only meager amounts of forage are available to large herbivores in arid regions. Similarity indices show that the three study sites are dissimilar with respect to frequency of occurrence and canopy cover of plants. The numbers of plant taxa varied among locations, with areas near man-made ponds showing the richest compositions. The B Pond and Gable Mountain Pond areas showed greatest similarity in plant frequency and canopy cover. The B-C Cribs area was the least similar of all sites.

Dietary habits of the mule deer in south-central Washington on *Artemisia tridentata/Poa sandbergii* associations (Daubenmire, 1970) have not been reported in the literature. Most authors have reported dietary habits of mule deer on bunchgrass rangelands,

which have some sagebrush and bitterbrush with understory species of bluebunch wheatgrass (*Agropyron spicatum*), cheatgrass, and sandberg bluegrass (Edgerton and Smith, 1971; Wilkins, 1957; Morris and Schwartz, 1957; Nellis and Ross, 1969; and Lovaas, 1958). These studies have been conducted in areas which receive more precipitation than the Hanford Site.

The mule deer select forbs as the mainstay of their diet at B Pond and Gable Mountain Pond areas. Shrubs were the second most common food item, while grasses were a minor part of the total diet. At B-C Cribs, shrubs were the major food item found in the pellets, with lesser amounts of forbs and grasses. In Montana, Wilkins (1957) found that summer forbs were the most important, that shrubs were of less importance, and that grass was least often eaten. Wilkins also found that bitterbrush was the most important species in the deer's diet during the fall. Elgerton (1971) showed that forbs were important in spring in eastern Oregon. However, with the decline of spring forbs, the amounts of grasses and shrubs in the diets of deer increased sharply. During fall, grasses and sedges were important, and shrubs became a major constituent of the diets in forested areas.

At Hanford, six forage species provided the mainstay of the mule deer diet from the B Pond habitat; three forage species made up most of the diet in B-C Cribs and Gable Mountain Pond habitats. Several species of plants were abundant, but rarely eaten. Some of these species were probably unpalatable, whereas others were not eaten because more preferred species were available. Short *et al.* (1966) have shown that the normal and predictable variations in plant chemistry caused by seasonal changes in plant phenology and physiology have important implications in the nutrition and physiology of deer. Choice of major forage species by the deer may be related to the nutrient requirements of the animals.

Dietary analyses of mule deer, when related to the availability of forage plants in the habitats, provide useful information in selecting plants for revegetation purposes at low level radioactive burial sites from nuclear energy facilities. Deer managers are reminded of the importance in revegetation practices to select plants not consumed by deer and thus discourage plant utilization at certain sites, particularly around ponds that contain nuclear effluents. The ultimate goal is to keep food chain transfers of radionuclides to a level as low as possible.

Acknowledgments

This study was conducted at Pacific Northwest Laboratories in Richland, Washington, and was supported by Rockwell Hanford Operations (RHO) as part of a program to document the potential for transporting waste radionuclides through biotic pathways. Many of the methods to analyze diet and vegeation were developed on the Arid Land Ecology Reserve under separate funding by the Department of Energy, under contract DE-AC06-76-RLO-1830.

The authors thank Marci Combs, Mark Rumble, Fern Nelson, and Virgil Charles for their helpful suggestions and technical assistance during this study. Thanks also are extended to Lee Rogers, John Cline, and Donald Paine for their critical reviews and technical advice. Special thanks are given to Richard M. Hansen and Terry Foppe at Colorado State University for dietary analyses of the deer pellets.

Literature Cited

Baumgartner, L. L., and A. C. Martin. 1939. Plant histology as an aid in squirrel food-habit studies. J. Wildl. Manage. 3:266-268.

Cline, J. F., D. W. Uresk, and W. H. Rickard. 1977. Plants and soil of a sagebrush community on the Hanford Reservation. Northw. Sci. 51:60-70.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northw. Sci. 33:43-64.

———. 1970. Steppe Vegetation of Washington. Wash. Agric. Exp. Stn. Tech. Bull. 62.

Edgerton, P. J., and J. G. Smith. 1971. Seasonal Forage Use by Deer and Elk on the Starkey Experimental Forest and Range, Oregon. U.S. Forest Service Research Paper, PNW-112.

Hajek, B. F. 1966. Soil Survey—Hanford Project in Benton County, Washington. BNWL-234. Battelle, Pacific Northwest Laboratories, Richland, Wash.

Hedlund, J. D. 1975. Trapping mule deer fawns in south-central Washington, 1969-1974. Northw. Sci. 49:153-157.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest, an Illustrated Manual. Univ. of Washington Press, Seattle.

Krueger, W. C. 1972. Evaluating animal forage preference. J. Range Manage. 25:471-475.

Lovaas, A. L. 1958. Mule deer food habits and range use, Little Belt Mountains, Montana. J. Wildl. Manage. 22:275-283.

Morris, M. S., and J. E. Schwartz. 1957. Mule deer and elk food habits on the National Bison Range. J. Wildl. Manage. 21:189-193.

Nellis, C. H., and R. L. Ross. 1969. Changes in mule deer food habits associated with herd reduction. J. Wildl. Manage. 33:191-195.

Oosting, H. J. 1956. The Study of Plant Communities. W. H. Freeman and Company, San Francisco, Calif.

Short, H. L., D. R. Dietz, and E. E. Remmenga. 1966. Selected nutrients in mule deer browse plants. Ecology 47:222-229.

Siegel, S. 1956. Non-parametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Snedecor, G. W., and W. C. Cochran. 1967. Statistical Methods. Iowa State Univ. Press, Ames.

Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. J. Range Manage. 21:264-265.

Uresk, D. W. 1978. Diets of the Black-tailed hare in steppe vegetation. J. Range Manage. 31: 439-442.

Wilkins, B. T. 1957. Range use, food habits, and agricultural relationships of mule deer, Bridger Mountains, Montana. J. Wildl. Manage. 21:159-169.

Received May 2, 1980
Accepted for publication September 19, 1980

David R. Bernard[1]

and

Eugene K. Israelsen
Utah Water Research Laboratory
Utah State University
Logan, Utah 84322

Inter- and Intrastream Migration of Cutthroat Trout (Salmo clarki) in Spawn Creek, a Tributary of the Logan River, Utah

Abstract

We investigated inter- and intrastream movements of fluvial cutthroat trout (*Salmo clarki*) within Spawn Creek and between this stream and the Logan River, Utah. From November 1973 through November 1975, we captured all migrants with a fish trap on Spawn Creek and tagged adult cutthroat trout. Monthly from July 1973 through November 1975, we electrofished parts of Spawn Creek and cold-branded all unmarked juveniles and adults. Also, we continuously measured water temperature and stream flows at the trap. During the spawning season in 1974, 39 cutthroat trout entered Spawn Creek and 23 left; and in 1975, 77 fish entered and 71 left the stream. Spawning migrants entered Spawn Creek when spring freshets from melting snow increased stream flows and turbidity. Tag returns from fishermen indicated adult cutthroat trout traveled to the Logan River after leaving Spawn Creek. In 1974, 229 and in 1975, 359 cutthroat trout fry left Spawn Creek in early fall when dwindling stream flows reduced habitat along stream margins. Migratory patterns of adults and fry show cutthroat trout use Spawn Creek for spawning and the Logan River for growing. Spawn Creek contains extensive spawning habitat with little deep-water habitat while the Logan River is its complement. In 1974 and 1975, respectively, 30 and 13 cutthroat trout (age 1 and older) constituted fall runs into Spawn Creek. Intrastream movements of cutthroat trout within Spawn Creek were extensive, with 35 percent of recaptured fish having moved from where released.

Introduction

Fluvial cutthroat trout (*Salmo clarki*) do not migrate in some watersheds (Diana and Lane, 1978; Miller, 1957) but do in others (Averett and MacPhee, 1972; Bjornn and Mallet, 1964; Kiefling, 1978; Wyatt, 1959). Whether migration occurs largely depends upon the distribution of spawning habitat. For example, in the upper Snake River, high flows and silt limit spawning in the river proper, while tributaries supply suitable spawning habitat (Kiefling, 1978). In contrast, Gorge Creek, Alberta, has ample spawning habitat and no migration (Miller, 1954; 1957).

In those watersheds with migrating fluvial cutthroat trout, the migratory pattern is basically the same. Tributaries are used as spawning and rearing areas, and main-stem rivers for growth and maturation. However, some deviations in the pattern occur from one watershed to another (Averett and MacPhee, 1972; Bjorn and Mallet, 1964; Hayden, 1967; and Wyatt, 1959). The triggering factor for migration differs from area to area. In Lookout Creek, cutthroat trout did not move until water temperatures in tributaries surpassed 5°C (Wyatt, 1959). In the upper Snake River, small trout left tributaries in winter during low air temperatures (Hayden, 1967). In Idaho streams, cutthroat trout migrate with greater frequency during high flows (Gebhards and Fisher, 1972).

[1]Present address Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska 99502.

Our study was designed to measure cutthroat trout migration within, into, and out of Spawn Creek, a tributary of the Logan River in northern Utah; to compare these movements with stream flows and water temperatures; and to propose possible causes of migratory behavior.

Study Area

Spawn Creek is a secondary tributary of the Logan River with Temple Fork the connecting stream (Fig. 1). Spawn Creek is primarily spring-fed with runoff adding significantly to flows only during spring snowmelt. The lower 1.8 km of Spawn Creek is a series of riffles and plunge pools caused by riparian shrubs (*Salix* sp.) partially damming the stream; rapids and abandoned beaver ponds dominate the upper 2.9 km of the stream. Rooted vegetation, mostly sedges (*Carex* sp.) and watercress (*Nasturium* sp.), occurs in beaver ponds and alongside riffles. Brook trout (*Salvelinus fontinalis*) inhabit higher elevations in Spawn Creek; brown trout (*Salmo trutta*) occur in lower elevations; cutthroat trout are ubiquitous.

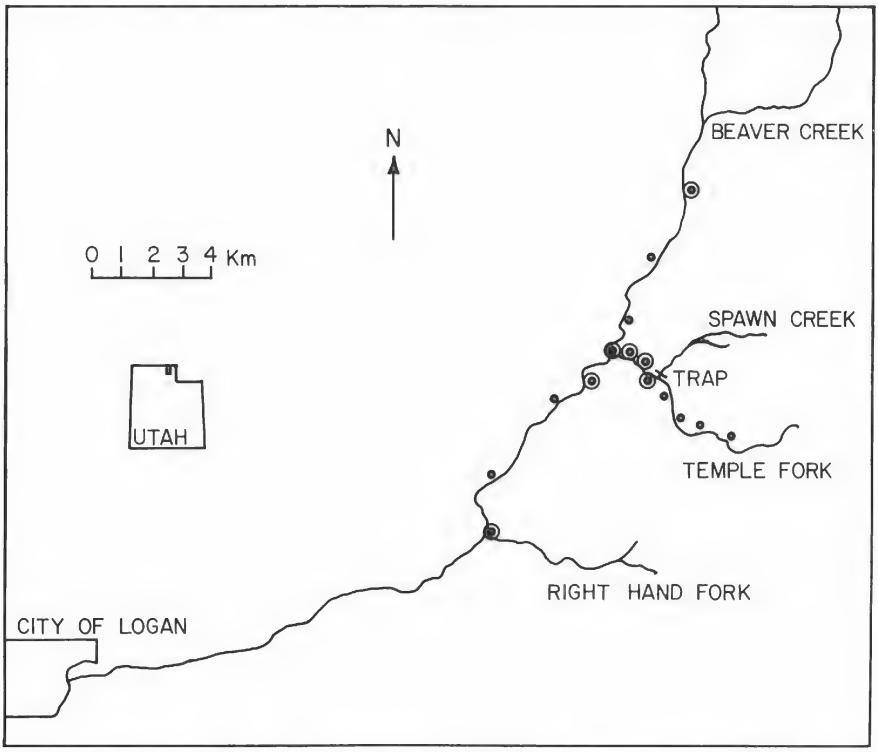


Figure 1. Logan River and major tributaries. Dots represent locations of tag-return boxes; circles denote boxes in which tags were found.

Methods

We constructed a two-way, all-weather fish trap .2 km above the mouth of Spawn Creek (Twedt and Bernard, 1976) and operated it from 21 November 1973 to 20

November 1975. Because the entire stream flowed through the trap, the trap captured all migrants except during 31 days from mid-June through mid-July 1974, when bedload sediments clogged screens and caused the trap to overflow, and during 10 days in winter when frazil ice caused overflowing. We removed fish from the trap daily to weekly, depending on frequency of fish movements or the need to clean the trap of sediments and leaf litter. All migrant fish were measured, and a scale sample was taken from each fish longer than 10 cm TL. Migrants longer than 20 cm TL were tagged with individually numbered dart tags (Dell, 1968); smaller fish were not marked. We erected 15 boxes at regular intervals along Temple Fork and the Logan River to receive dart tags from fishermen (Fig. 1) and checked boxes monthly during the fishing seasons (June to December).

From July 1973 to November 1975 we electrofished randomly selected 100-m segments of Spawn Creek with a portable 300 watt AC generator converted to variable voltage pulsed DC. In any one sample, we electrofished .5 to 3.0 km of stream. Captured fish longer than 10 cm TL were cold-branded with individually identifiable numbers (Everest and Edmundson, 1967) and returned to the 100-m segment from which we captured them. Trap data taken just after release of fish in stream segments indicated 100 m was sufficient distance for fish to recover from handling and to maintain their position in the stream. Therefore, we considered branded fish to have moved only if they traveled beyond the 100-m segments adjacent to their last segment of release. In late June 1974 we electrofished the lower 4.6 km of Temple Fork for marked fish.

To simplify our analysis, we grouped ages of cutthroat trout captured at the trap and in electrofishing surveys into three categories: adults (age group III and older), juveniles (age group I and II), and young (age group 0). We determined fish age by comparing individual fish lengths to length-frequency of all captured fish and by counting annuli on fish scales.

From 2 October 1973 to 31 May 1975 we continuously measured stream flows and water temperatures 3 m below the fish trap with a trapezoidal cutthroat flume and a 31-day recording thermometer. We calculated mean daily stream flow and mean daily water temperature as the midpoints between daily extremes for each hydrographic factor.

Results

Mean daily stream flow ranged from .14 m^3/sec to .38 m^3/sec in 1974 and from .15 m^3/sec to .45 m^3/sec in 1975 (Fig. 2). Stream flows varied little hourly, except in late April 1974 and mid-May 1975, when freshets of melted snow temporarily increased stream flows and Spawn Creek became atypically turbid. Mean daily water temperatures ranged from 1.1°C to 10.6°C in 1974 and 1.7°C to 9.4°C in 1975 (Fig. 3). Unlike stream flows, mean daily water temperatures varied greatly from day to day and even from hour to hour. Daily extremes 8°C apart were not uncommon during summer. On five winter nights in 1974 and four winter nights in 1975, frazil ice formed in the lower .4 km of Spawn Creek. During late December to early February, anchor and frazil ice occurred almost nightly in Temple Fork below its confluence with Spawn Creek. We saw no anchor or frazil ice on the Logan River below its confluence with Temple Fork.

Most adult cutthroat trout migrated into and out of Spawn Creek during the spawning season from April through July (Fig. 4). In 1974, 31 adults (24 males and 7 females) and 8 juveniles immigrated with highest frequency during the first week in

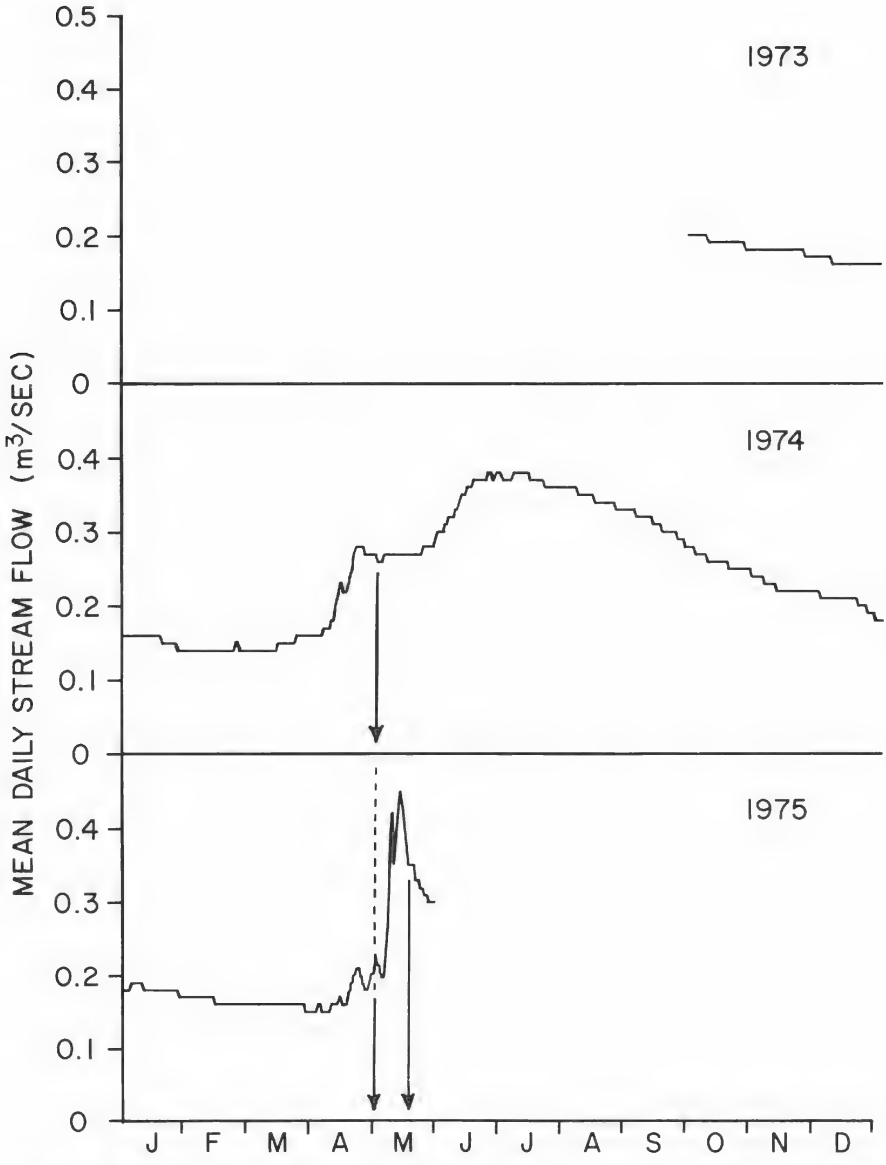


Figure 2. Stream flows measured at the fish trap on Spawn Creek, Utah. Mean daily stream flows are midway between daily extremes, rounded to the nearest .01 m^3/sec. Arrows mark weeks of highest frequency of cutthroat trout migrating into Spawn Creek during the spawning runs in 1974 and 1975.

May, just after freshets of melted snow increased mean daily stream flows (Fig. 2). In the same year, 18 adults (7 males, 6 females, 5 sex unknown) and 5 juveniles left Spawn Creek. In 1975, 50 adult cutthroat trout (26 males, 19 females, 5 sex unknown)

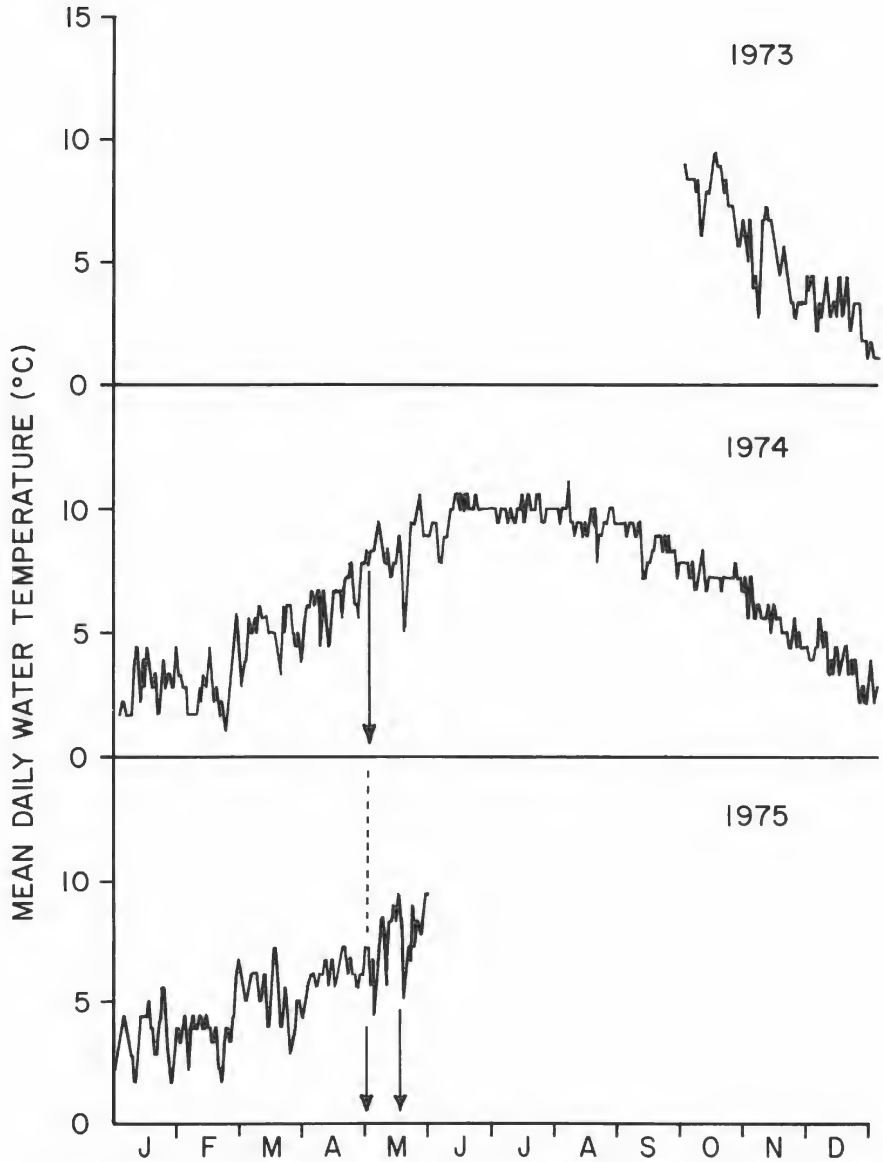


Figure 3. Water temperatures measured at the fish trap on Spawn Creek, Utah. Mean daily water temperatures are midway between daily extremes rounded to the nearest .1°C. Arrows mark weeks of highest frequency of cutthroat trout migrating into Spawn Creek during the spawning runs in 1974 and 1975.

and 27 juveniles entered Spawn Creek with highest frequency during the third week in May, again just after mean daily stream flows peaked (Fig. 2). In the same year, 56 adult cutthroat trout (20 males, 24 females, 12 sex unknown) and 15 juveniles left

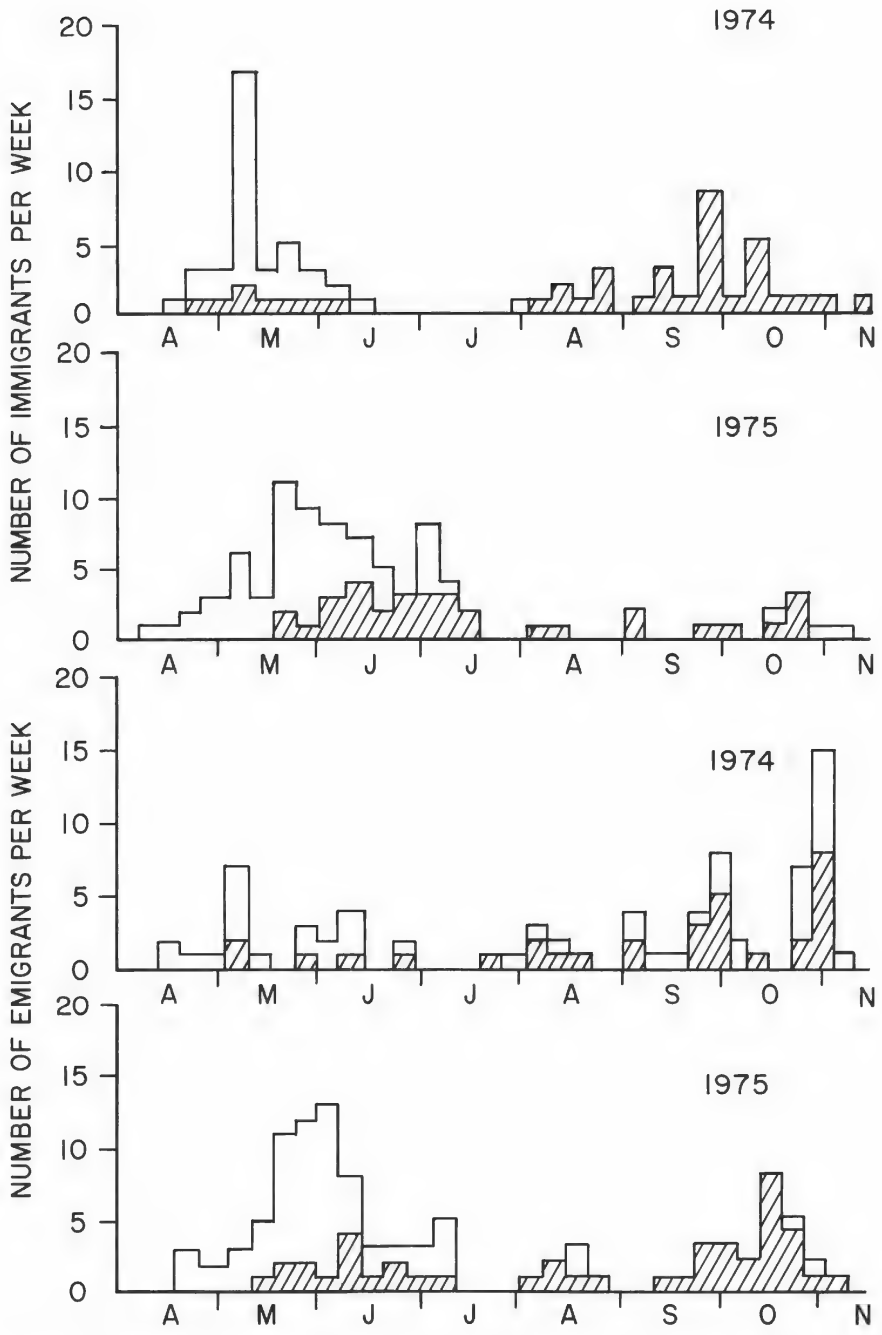


Figure 4. Histograms of upstream (immigrating) and downstream (emigrating) movements of cutthroat trout observed at the fish trap on Spawn Creek. Lined areas correspond to movements of juveniles (age I and II) and clear areas to adults (III and older).

Spawn Creek. In both years, highest frequencies of male cutthroat trout entering and leaving Spawn Creek occurred one week before those for females. In 1974 and 1975, little spawning activity occurred after mid-June.

Many cutthroat trout also migrated into and out of Spawn Creek from August to November. In 1974, 30 juveniles immigrated into Spawn Creek with highest weekly frequency the first week in October (Fig. 4), and in 1975, 10 juvenile and three adult cutthroat trout moved into Spawn Creek. Twenty-five juveniles left the stream in 1974, and 29 in 1975.

From June through December, 229 young in 1974 and 359 young in 1975 left Spawn Creek (Fig. 5). The highest weekly frequency occurred in the last week in September. In winter and spring, fewer young left Spawn Creek as one-year olds (14 in 1974 and 26 in 1975). No young migrated into Spawn Creek.

Of the 226 branded cutthroat trout we recaptured, 35 percent were recovered beyond the 100-m segments adjacent to where they were last released, 19 percent at the trap, and 46 percent in the segment where they were last released (Table 1). Most moving fish were adults (74 percent). Electrofishing gear selects larger fish and cold-brands fade faster on smaller, faster growing fish; these factors kept our probability of recapturing and recognizing branded juveniles lower than adults, thereby inflating the adult fraction of the moving population we observed. Frequencies of upstream and downstream movements were approximately equal for both adults and juveniles. Of those fish traveling both up and downstream during our study, we observed 71 percent traveling upstream after their first release. We recaptured 79 fish moving upstream 49 times (median distance 650 m) and downstream 55 times (median distance 450 m). The longest movements made by fish not captured at the trap were 2.8 km upstream and 2.4 km downstream.

TABLE 1. Number of branded cutthroat trout recaptured by electrofishing in Spawn Creek from August 1974 to November 1975.

Age	Total	Non-migrants	Interstream migrants	Intrastream migrants	No. separate migrations[1] Upstream	Downstream
Adults	125	35	31	59	40	43
Juveniles	101	70	12	19	9	12
Total	226	105	43	78	49	55

[1]A migrant can exhibit more than one migration by switching direction of travel.

Data from tag boxes and on migrants recaptured in Temple Fork indicated adults migrate through Temple Fork to the Logan River. Of 83 cutthroat trout tagged, we recovered 11 tags, eight along Temple Fork below its confluence with Spawn Creek and three along the Logan River (Fig. 1). We recovered no tags from this study in boxes on Temple Fork upstream of its confluence with Spawn Creek. Fishermen did fish upper Temple Fork and did deposit tags; in this area we recovered many tags used to mark rainbow trout (*Salmo gairdneri*) in a previous study on Temple Fork. While electrofishing Temple Fork, we recovered only one tagged migrant 1.0 km below the mouth of Spawn Creek; we tagged the fish seven days earlier at the trap. We captured no branded fish while electrofishing Temple Fork. During our study, 10 "tagged" fish returned to the trap after leaving Spawn Creek; all 10 had lost their tags but retained tagging scars.

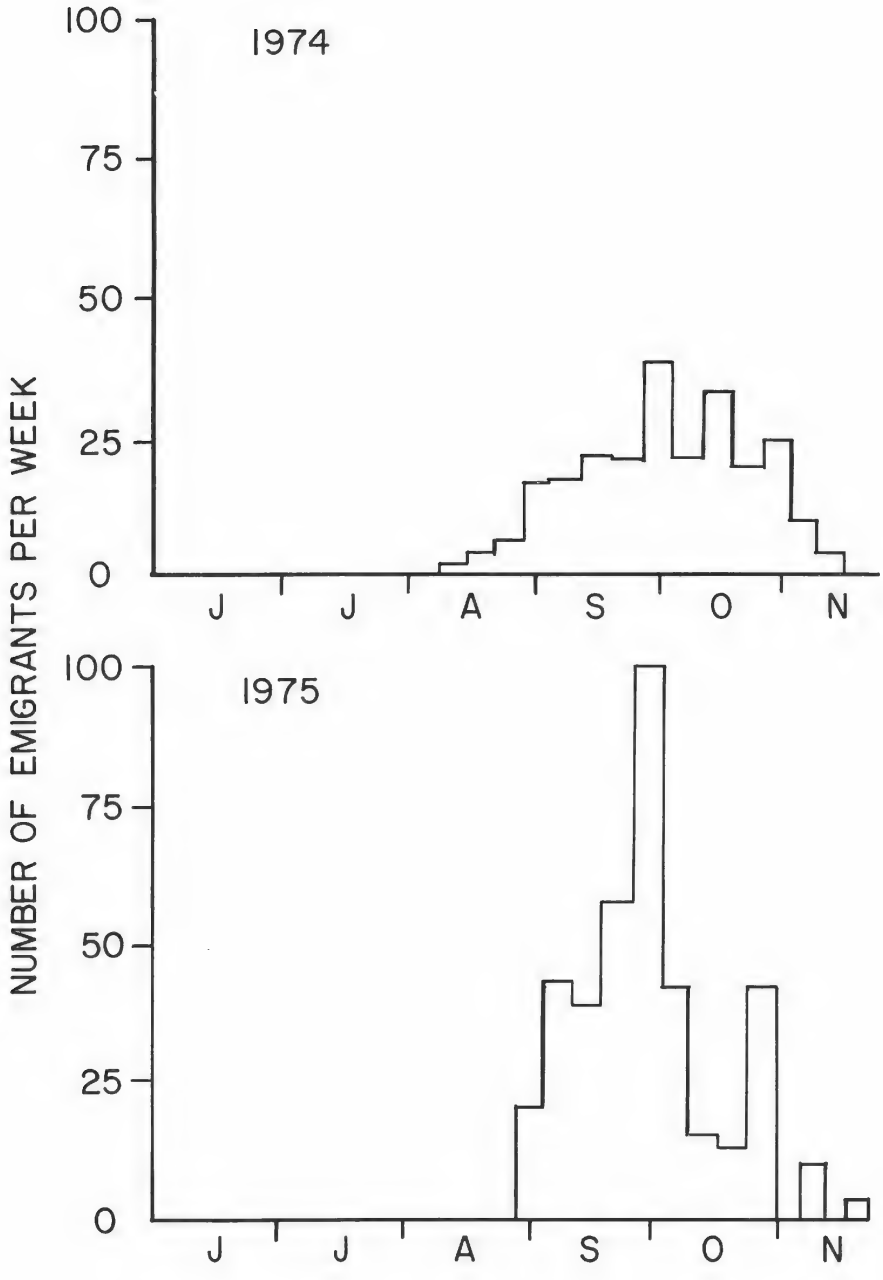


Figure 5. Histograms of downstream (emigrating) movements of young cutthroat trout (age 0) observed at the fish trap on Spawn Creek.

Discussion

Cutthroat trout are not endemic to Spawn Creek or to Temple Fork but migrate between Spawn Creek and the Logan River. Tag returns indicate adults grow and mature in the Logan River, migrate into Spawn Creek, spawn, and return to the Logan River. Most young cutthroat trout remain in Spawn Creek a few months after hatching; then they also migrate to the Logan River. Young cutthroat trout from Spawn Creek probably overwinter in the Logan River. Swift currents and several culverts in Temple Fork make upstream travel by young difficult, and anchor and frazil ice seen in this study and others (Pearson and Kramer, 1972) preclude overwintering by fish in Temple Fork below the mouth of Spawn Creek. Fleener's (1951) observation of numerous small cutthroat trout in the Logan River around the mouth of Temple Fork also supports the hypothesis that the former stream is the terminus for young migrating from Spawn Creek. Cutthroat trout migrate between Spawn Creek and the Logan River because Spawn Creek has gravel for spawning and the Logan River space for growing. In the Salmon River watershed, higher-order streams are deep, wide, and have rubble in their stream channels, while lower order streams are shallow, narrow, and have predominantly gravel as substrates (Platts, 1979); this relationship between stream order and habitat also pertains to the Logan River watershed. Gravels suitably sized for spawning are concentrated in Spawn and Beaver Creeks (Fleener, 1951). Most gravels in lower Spawn Creek are within size ranges (2.0 cm to 7.8 cm) preferred by cutthroat trout in other watersheds (Cope, 1957; Hayden, 1967). While substrates in the Logan River are mostly boulders, this stream contains most of the deep-water, ice-free habitat in the watershed.

In most migratory populations of cutthroat trout, young leave natal streams during their first summer (Benson, 1960; Snyder and Tanner, 1960; Wyatt, 1959). Trap overflow in 1974 did not allow us to determine if young migrated out of Spawn Creek from mid-June through mid-July, but in 1975 no young cutthroat trout left Spawn Creek until early fall, well after emerging from redds, much like young in tributaries of the Snake River (Hayden, 1967). Boussu (1954) and Hayden (1967) reported that young cutthroat trout migrated out of tributaries in winter when streamside vegetation froze, thereby reducing cover. Young cutthroat trout also leave Spawn Creek because of reduced habitat, but do so earlier in the fall. Electrofishing Spawn Creek indicated young reside only in quiet water in streamside vegetation. In early fall, water recedes from streamside aquatic plants, and any resident fish must move into faster water.

In our and other studies, adult and juvenile cutthroat trout migrated into tributaries from main-stem rivers in the fall (Benson, 1960; Bernard, 1976; Hayden, 1967; and Wyatt, 1959). We found no explanation for this migration. The run is not a spawning run; most migrants were immature, and fish migrated well after the spawning season. Many juveniles migrated into Spawn Creek with spawning adults as they do in other watersheds (Hayden, 1967; Wyatt, 1959). If juvenile cutthroat trout migrate with spawning fish, their fall run into Spawn Creek may be caused by spawning brown trout migrating into the stream (Bernard, 1976). However, in other watersheds with known, fall migrating cutthroat trout, no fall spawners are present.

Stream flow, not water temperatures, determines the relative frequency of cutthroat trout spawning migration into Spawn Creek during the spring; fish move with the greatest frequency just after the highest spring flows. Gebhards and Fisher (1972) state similar relationships exist between high flows and migrating cutthroat trout in

Idaho streams. Cope (1956) believes high stream flows and associated turbidity provide cover for migrating adfluvial cutthroat trout in other Utah streams. Because recorded hourly and mean daily water temperatures were so variable, no difference in spring water temperatures between 1974 and 1975 was detectable, but cutthroat trout immigrated into Spawn Creek two weeks earlier in 1974.

Resident cutthroat trout within Spawn Creek behave unlike resident cutthroat trout in watersheds with no migration. Two hypotheses explain why resident cutthroat trout move within Spawn Creek. The first is that migrants displace residents. In pools and adjoining riffles, cutthroat trout establish dominant and subdominant positions based on their size (Griffiths, 1972). Any spawning migrant passing through will disrupt these hierarchies, thereby displacing fish. The second hypothesis is that Spawn Creek contains no resident population. All cutthroat trout leave the stream sooner or later, and fish within the stream at any one time are those that will leave later. In 1975, more adult cutthroat trout left Spawn Creek after spawning than entered the stream before, indicating some "residents" became migratory.

We do not know how important recruitment from Spawn Creek is to the cutthroat trout population in the Logan River watershed, but we do know that migration is of paramount importance to the population dynamics of cutthroat trout in Spawn Creek. If Spawn Creek and other tributaries play similar roles in the Logan River watershed, these tributaries and the quality of their habitat are important to managing this fishery.

Acknowledgments

We are indebted to the late Dr. Robert Kramer for the original inspiration for this project, Drs. Tom Twedt and Robert Hill for their engineering expertise, Craig Reger for his long hours of assistance, Drs. James Hall and Howard Horton for their review of this work, and the Utah Water Research Laboratory for their patience and support.

Literature Cited

Averett, R. C., and C. MacPhee. 1972. Distribution and growth of indigenous fluvial and adfluvial cutthroat trout (*Salmo clarki*), St. Joe River, Idaho. Northw. Sci. 45:38-46.

Benson, N. G. 1960. Factors influencing production of immature cutthroat trout in Arnica Creek, Yellowstone Park. Trans. Amer. Fish. Soc. 89:168-175.

Bernard, D. R. 1976. Reproduction by adfluvial salmonids in Spawn Creek, Cache County, Utah. Utah State Univ., Logan, Utah. M. S. thesis.

Bjornn, T. C., and J. Mallet. 1964. Movements of planted and wild trout in an Idaho River system. Trans. Amer. Fish. Soc. 93:70-76.

Boussu, M. F. 1954. Relationship between trout populations and cover on a small stream. J. Wild. Mgt. 18:229-239.

Cope, O. B. 1956. Some migration patterns in cutthroat trout. Proc. Utah Acad. Sci., Arts, and Lett. 33:113-118.

———. 1957. The choice of spawning sites by cutthroat trout. Proc. Utah Acad. Sci., Arts, and Lett. 34:73-79.

Dell, M. B. 1968. A new fish tag and rapid cartridge-fed applicator. Trans. Amer. Fish. Soc. 97(1): 57-59.

Diana, J. S., and E. D. Lane. 1978. The movement and distribution of Paiute cutthroat trout, *Salmo clarki seleniris*, in Cottonwood Creek, California. Trans. Amer. Fish. Soc. 107:444-448.

Everest, F. H., and E. H. Edmundson. 1967. Cold branding for field use in marking juvenile salmonids. Prog. Fish-Cult. 29:175-176.

Fleener, G. C. 1951. Life history of the cutthroat trout, *Salmo clarki* Richardson, in the Logan River, Utah. Trans. Amer. Fish. Soc. 81:235-248.

Gebhards, S., and J. Fisher. 1972. Fish passage and culvert installation. Idaho Fish and Game Dept.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. J. Fish. Res. Board Can. 29:265-273.

Hayden, P. S. 1967. The reproductive behavior of the Snake River cutthroat trout in three tributary streams in Wyoming. Wyo. Game and Fish Comm., Coop. Res. Proj. No. 4.
Kiefling, J. W. 1978. Studies on the ecology of the Snake River cutthroat trout. Wyo. Fish and Game Dept., Fish. Tech. Bull. No. 3.
Miller, R. B. 1954. Movements of cutthroat trout after different periods of retention upstream and downstream from their homes. J. Fish. Res. Board Can. 11:550-558.
———. 1957. Permanence and size of home territory in stream dwelling cutthroat trout. J. Fish. Res. Board Can. 14:687-691.
Pearson, W. D., and R. H. Kramer. 1972. Drift and production of two aquatic insects in a mountain stream. Ecol. Mon. 42:366-385.
Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries 4:5-9.
Snyder, G. R., and H. A. Tanner. 1960. Cutthroat trout reproduction in the inlets to Trapper's Lake. Colo. Dept. Fish and Game, Tech. Bull. No. 7.
Twedt, T. M., and D. R. Bernard. 1976. An all-weather, two-way fish trap for small streams. Cal. Fish and Game 62:21-27.
Wyatt, B. 1959. Observations on the movements and reproduction of the Cascade form of cutthroat trout. Oregon State College, Corvallis. M. S. thesis.

Received June 20, 1980
Accepted for publication October 15, 1980

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian D. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Andrew V. Corry
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
F. A. Gilfillan
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Frank D. Nicol
William A. Rockie
Francis J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
S. C. Vandecaveye
Richard B. Walker
D. J. Wort

1982 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1982 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Gonzaga University, Spokane, Washington
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Malaspina College, Nanaimo, British Columbia, Canada
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Northern Montana College, Havre, Montana
Oregon College of Education, Monmouth, Oregon
Oregon Institute of Technology, Klamath Falls, Oregon
Oregon State University, Corvallis, Oregon
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
Saint Martin's College, Lacey, Washington
Seattle Central Community College, Seattle, Washington
Seattle Pacific University, Seattle, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
South Seattle Community College, Seattle, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Oregon, Eugene, Oregon
University of Puget Sound, Tacoma, Washington
University of Victoria, Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State University, Pullman, Washington
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Yakima Valley College, Yakima, Washington

1982 Sustaining Individual Members

Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Robert L. Carr, Cheney, Washington
Susan G. Conrad, Corvallis, Oregon
George W. Douglas, Victoria, British Columbia, Canada
Bruce Ettling, Vancouver, Washington
George R. Fahnestock, Seattle, Washington
Gerald H. Haddock, Wheaton, Illinois
Frederick C. Hall, Portland, Oregon
Charles R. Hatch, Moscow, Idaho
Robert J. Jonas, Pullman, Washington
Barry L. Keller, Pocatello, Idaho
Denis L. Lavender, Corvallis, Oregon
William L. Lester, Arcata, California
William A. Long, Crescent City, California
Albert L. Merkel, Moscow, Idaho
Daniel F. Milam, Bellevue, Washington
Emmett B. Moore, Jr., Richland, Washington
Milton A. Mosher, Pullman, Washington
William A. Rickard, Richland, Washington
Lee E. Rogers, Richland, Washington
Raymond A. Soltero, Cheney, Washington
Ronald J. Taylor, Bellingham, Washington
Daniel W. Uresk, Rapid City, South Dakota
Shepard M. Zedaker, Christiansburg, Virginia

Northwest Science

Washington State University

Pullman, Washington 99164

Alfred R. Halvorson
Agronomy Dept.
Washington State Univ.
Pullman, WA 99164

Associate Editors

Botany	Kenneth C. Swedberg	Eastern Washington University
Forestry	Arthur R. Tiedemann	U.S. Forest Service
Geology	Franklin F. Foit, Jr.	Washington State University
Soils	Stanley P. Gessel	University of Washington
Zoology	Irven O. Buss	Washington State University

Change of Address Send change of address notice to the Treasurer as listed on the inside front cover.

Instructions to Authors The pages of Northwest Science are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. At least one of the authors of papers submitted for publication must be a member of the Northwest Scientific Association. Manuscripts (original typescript plus two copies) should be submitted to the Editor, Northwest Science, Washington State University, Pullman, Washington. Prior to submitting manuscripts, authors should request a copy of "Instructions to Authors" from the Editor.

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164, U.S.A.

Volume 56, Number 3

August 1982

Northwest Science

159 Wolverines in Western Wyoming
John H. Hoak, J. L. Weaver, and T. W. Clark
162 The Distribution of **Artemisia rigida** in Washington: A Challenge to Ecology and Geology
R. Daubenmire
165 Taste Aversion Conditioning in Free Ranging Raccoons **(Procyon lotor)**
Lowell K. Nicolaus, Todd E. Hoffman, and Carl R. Gustavson
170 Effects of Volcanic Ash on Soil Nitrogen Mineralization and Accompanying CO_2 Production
J. L. Smith, E. J. Owens, and B. L. McNeal
176 Siphonaptera: Host Records from Crater Lake National Park, Oregon
Robert A. Gresbrink and David D. Hopkins
180 A Comparison of Treeless Areas in the Forested Foothills of the Cascade Mountains of Western Washington
Kern Ewing
190 The Distribution and Thickness of Volcanic Ash in Montana
Thomas J. Nimlos and Hans Zuuring
199 Dispersal, Daily Activity, and Home Range of Coyotes in Southeastern Idaho
Roger A. Woodruff and Barry L. Keller
208 Cervid Activity Patterns in Relation to Foraging Constraints: Western Washington
Thomas A. Hanley
218 Early Cenozoic Geology of Central Washington State: I. Summary of Sedimentary, Igneous, and Tectonic Events
Randall L. Gresens
230 Age Determination and Age-Specific Reproduction in Belding's Ground Squirrels
David B. Costain and B. J. Verts
236 Habitat Use by Porcupines in a Ponderosa Pine/Douglas-fir Forest in Northeastern Oregon
Graham W. Smith
241 Population Structure of the Crab **Hemigrapsus oregonensis** (Brachyura, Grapsidae) in Yaquina Bay Estuary, Oregon. II. Vertical Distribution, Biomass, and Production
Robert E. Batie
250 Primary Production and Canopy Cover in Bitterbrush-Cheatgrass Communities
W. H. Rickhard and R. H. Sauer
257 Publication Announcement: 1981 Corvallis Forestry Symposium
257 Errata: Helvey, J. D., and W. B. Fowler. Northw. Sci. 56:27-33
257 Errata: Van Vuren, D., and S. E. Thompson, Jr. Northw. Sci. 56:131-135

Official Publication of the Northwest Scientific Association

US ISSN 0029 344X

Northwest Science

Volume 56, Number 3, August 1982

The Northwest Scientific Association is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to Northwest Science, is open to individual persons for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 3000 students or more, $40. All other subscribers, $20 per year. Sustaining membership, $25 per year for individual persons and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Payment should be made to the Treasurer.

Editor **John W. Weber**
Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164-2910

Officers of the Association

President **John H. Perkins**
The Evergreen State College
Olympia, Washington (1983)

Vice-President **Stephen F. Arno**
USDA Forest Service
Missoula, Montana (1983)

Secretary **Robert L. Carr**
Eastern Washington University
Cheney, Washington (1984)

Treasurer **Robert J. Jonas**
Department of Zoology
Washington State University
Pullman, Washington 99164-4220
(1983)

Past President **James R. Chambers**
Walla Walla College
College Place, Washington (1982)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Black
University of British Columbia
Vancouver, British Columbia
(1985)

Charles R. Hatch
University of Idaho
Moscow, Idaho (1983)

Janet E. Hohn
U.S. Fish and Wildlife Service
Portland, Oregon (1983)

Denis P. Lavender
Oregon State University
Corvallis, Oregon (1984)

Roger del Moral
University of Washington
Seattle, Washington (1983)

Don Minore
U.S. Forest Service
Corvallis, Oregon (1984)

Richard J. Naskali
University of Idaho
Moscow, Idaho (1984)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

Ronald H. Sauer
Battelle Northwest Laboratories
Richland, Washington (1984)

Steven R. Seavey
Lewis and Clark College
Portland, Oregon (1985)

Kareen Sturgeon
Linfield College
McMinnville, Oregon (1985)

J. Mary Taylor
2718 SW Old Orchard Road
Portland, Oregon 97201
(1983)

Robert Zasoski
University of Washington
Seattle, Washington (1984)

Donald B. Zobel
Oregon State University
Corvallis, Oregon (1983)

*Term of office expires in the year given in parentheses

PUBLISHED QUARTERLY BY WASHINGTON STATE UNIVERSITY PRESS
WITH COLLABORATION OF NORTHWEST SCIENTIFIC ASSOCIATION

John H. Hoak[1]

Biota-Research and Consulting
P. O. Box 2705
Jackson, Wyoming 83001

J. L. Weaver

Bridger-Teton National Forest
P.O. Box 1888
Jackson, Wyoming 83001

and

T. W. Clark

Department of Biology
Idaho State University
Pocatello, Idaho 83209

Wolverines in Western Wyoming

Abstract

New records of the wolverine (*Gulo gulo*) from western Wyoming during the past two decades suggest a population increase for this region.

Although the wolverine is considered rare and is protected by Wyoming Game and Fish Department (1977), its status in western Wyoming remains uncertain (Weaver and Clark 1979). This note reviews historical literature and presents 50 new wolverine reports (Fig. 1) for western Wyoming, not including Yellowstone National Park.

According to Coues (1877:49), "Mr. C. Hart Merriam . . . procured a specimen on the Yellowstone River, Wyoming, in August, 1872." Thomas (1952) states that a Mr. W. H. Hill treed with dogs and shot a male wolverine in January 1899 near Kendall, Wyoming. Long (1965) listed only eight additional reports for 1900-1960, all from northwestern Wyoming. Houston (1978) recorded 27 wolverine reports in and immediately adjacent to Yellowstone National Park 1970-1978. Winter distribution of wolverines in the Park generally coincided with ungulate winter ranges where carrion was available.

We compiled recent reports from 1) field interviews with outfitters and other backcountry users during summer and fall, 1977-1979; 2) telephone interviews with and written inquiries of trappers, hunters, outfitters, and other experienced backcountry users; and 3) records of Wyoming Game and Fish Department (WGF), Grand Teton National Park (GTNP), and Bridger-Teton National Forest (BTNF). Reports were evaluated according to the reliability of the observer, conditions of the observation, and/or the quality of detail provided. Numerous reports were omitted from this note for lack of detail, but all examined fell within the geographic area delineated herein. Details of reports are available from the authors.

---

[1]Present address: Miner Route, Emigrant, Montana 59027.

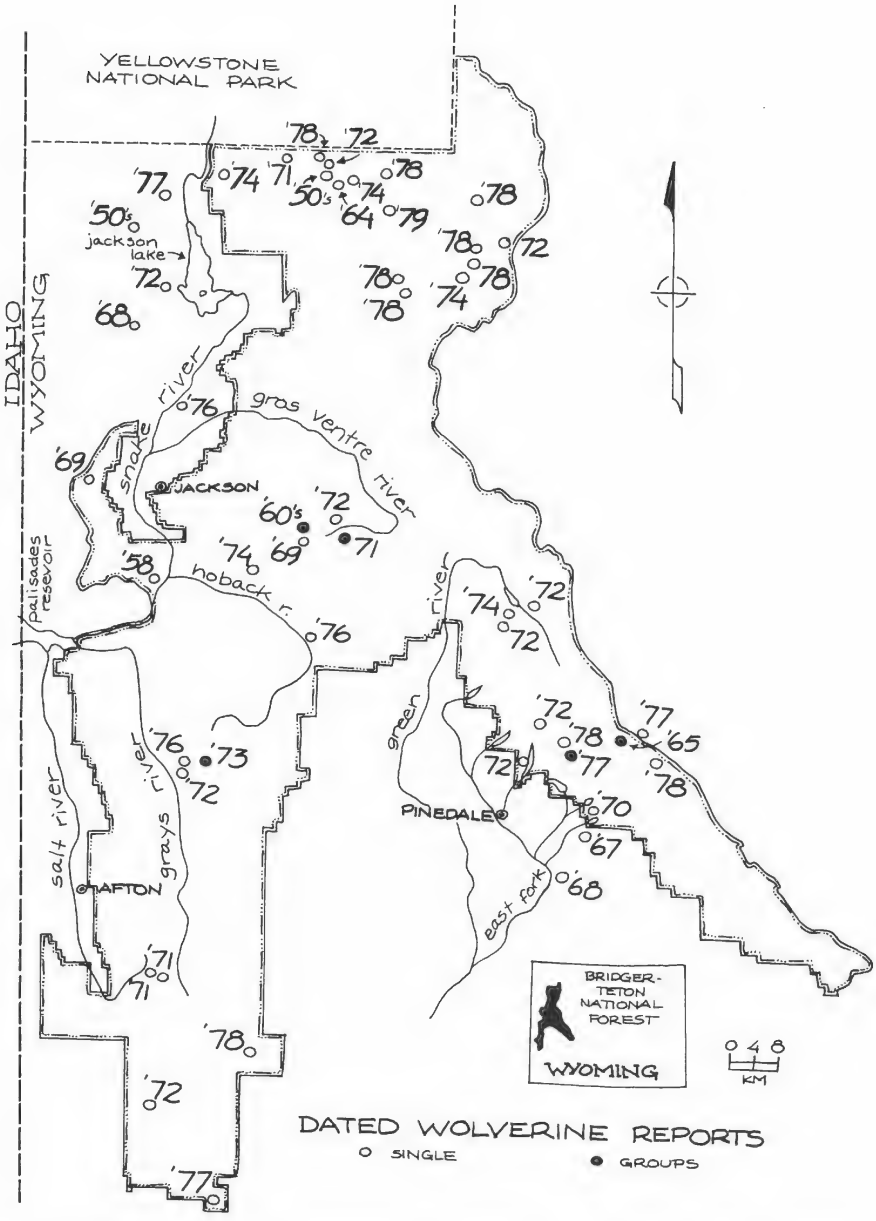


Figure 1. Location and year of 50 new wolverine reports in western Wyoming. Open circles indicate solitary animals; shaded circles, two or more wolverines (usually a family).

Wolverines occurred throughout the major mountain ranges of western Wyoming (Fig. 1), including areas farther south than previously reported. The apparent increase

of reports may reflect increased human use of remote areas, an extension of wolverine range, or both. We concur with Houston (1978) that the ban on poisons for predator control on Federal lands (Executive Order No. 11643) should benefit carrion-feeders such as the wolverine.

Acknowledgments

We thank personnel of the WGF, GTNP, and BTNF for providing reports. Information was gathered during research funded by Boone and Crockett Club, BTNF, National Rifle Association, and Northwest Scientific Association.

Literature Cited

Coues, E. 1877. Fur-bearing animals: a monograph of North American Mustelidae. . . . U.S. Geol. Surv. Terr., Misc. Publ. No. 8.

Houston, D. B. 1978 (Rev.). Cougar and wolverine in Yellowstone National Park. Res. Note No. 5. Yellowstone National Park.

Long, C. A. 1965. The mammals of Wyoming, pp. 493-758 *in* Univ. of Kansas Publ. V. 14, No. 18. Lawrence, Kans.

Thomas, E. M. 1952. The fur-bearing mammals of Wyoming—the common wolverine. Wyoming Wildl. 16:24-27.

Weaver, J. L., and T. W. Clark. 1979. Mammals, pp. 63-76 *in* T. W. Clark and R. D. Dorn (eds.), Rare and endangered vascular plants and vertebrates of Wyoming. Biota Publ., Jackson, Wyo.

Wyoming Game and Fish Department. 1977. Current status and inventory of wildlife in Wyoming. Wyo. Game and Fish Dept. Cheyenne.

Received July 2, 1980
Accepted for publication April 8, 1981

R. Daubenmire
636 Interlachen Drive
Sorrento, Florida 32776

The Distribution of *Artemisia rigida* in Washington: A Challenge to Ecology and Geology

Abstract
The distribution of *Artemisia rigida* in eastern Washington reveals some peculiar features which suggest a high degree of sensitivity to the substrate, climate, and/or geologic history of the area.

Early in the course of investigating the vegetation of eastern Washington (Daubenmire and Daubenmire 1968, Daubenmire 1970), some peculiarities in the distribution of *Artemisia rigida* (Nutt.) Gray became apparent, and thereafter dots were accumulated on a map (Fig. 1) to show the location of all stands that were seen during subsequent field work.

This dwarf shrub is everywhere restricted to shallow stony soils over bedrock, but has been seen only where the parent rock is basalt. Other rock types occur in the region, but even where these are contiguous with basalt outcroppings, the plant fails to colonize them.

Another major peculiarity involves the absence of the plant in a large area centered in Franklin County (Fig. 1). The existence of this void is especially challenging, and four possible working hypotheses for its explanation are suggested.

First, since the plant is sensitive to the difference between basalt and granitic bedrock, the chemical composition of the basalt outcrops in the void may differ from those of the surrounding area in some subtle manner. However, the Columbia Basin of eastern Washington was floored with nearly horizontal basalt flows, with later down-warping accentuating the intermountain basin, so this hypothesis is suspect. Planting seeds from the adjacent area on outcrops within the void would be a sound experimental procedure for testing this hypothesis, as well as the two which follow.

Second, physical features of the basalt may be more critical than its chemistry, for in many places *Artemisia rigida* gives way abruptly to stands of *Eriogonum niveum* on what appears to be the same homogeneous expanse of basaltic outcrop. Experiments (Daubenmire 1970) indicate that soil chemistry or antagonism are not involved at these ecotones, and it has been suggested that perhaps the jointing pattern of the basalt beneath the thin stony soil profile may differ critically.

Third, the climate of the void, which coincides approximately with the lower part of the Columbia Basin, might be too hot or too dry for *Artemisia rigida.* But this hypothesis seems ruled out by the existence of those stands close to the Columbia River in the northeastern corner of Benton County, and especially by the plants close to this river in Klickitat County. Both sites are lower in altitude, therefore probably either hotter or drier than parts of the void. Still other subtle climatic conditions may indeed be important, as suggested by the abundance of the shrub to the east of the Blue Mountains, whereas it appears to be completely absent on the west slopes of these mountains

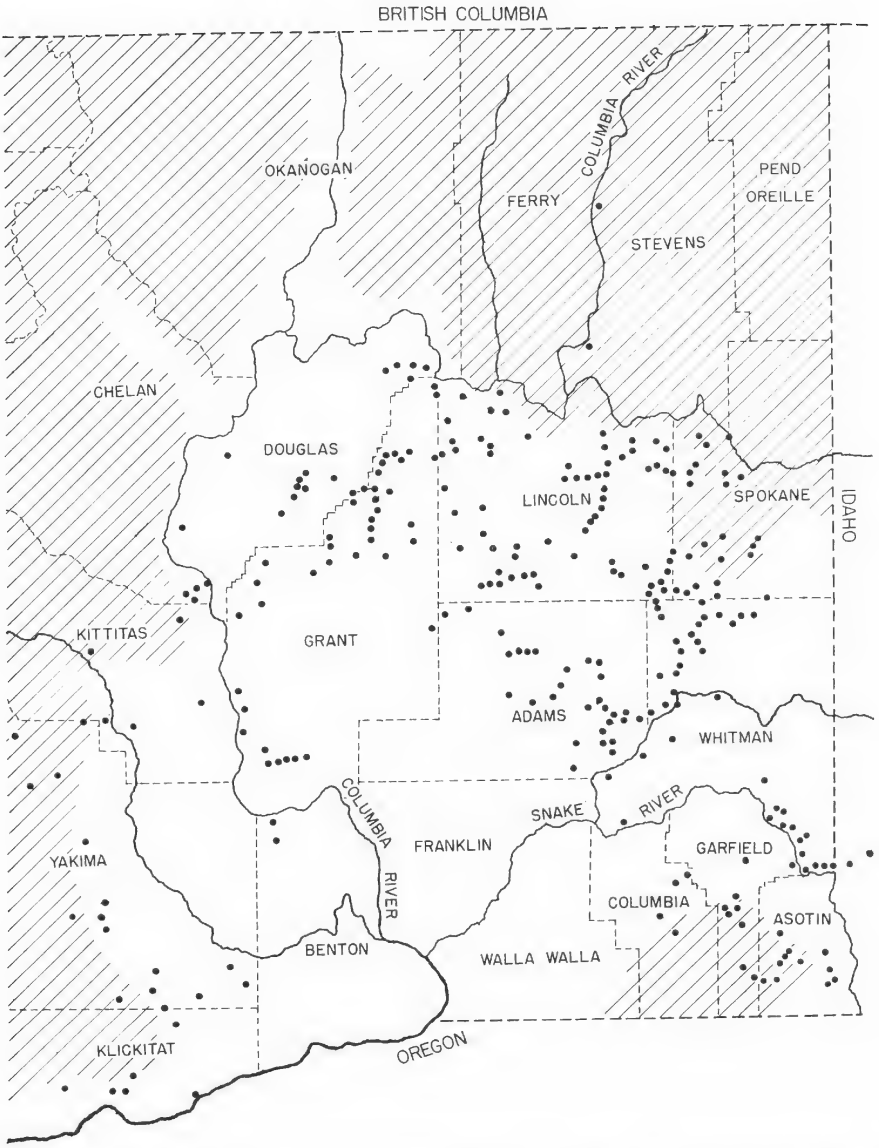


Figure 1. Distribution of *Artemisia rigida* as observed in Eastern Washington and adjacent Idaho.

at the same latitude. Furthermore, on the east slope of the Cascade Mountains the plant spans a climatic range from the *Pseudotsuga menziesii* belt at 1320 m down to the *Artemisia tridentata/Agropyron spicatum* belt at 190 m, whereas in eastern Washington it is completely absent over a large tract which exhibits a homologous vegetation catena.

Fourth, an historic factor may be involved. The vacant area in the range coincides at least roughly with the area below about 400 m, which is the area covered by glacial Lake Lewis that may have formed repeatedly during glacial times (Bretz *et al.* 1956,

McMacken 1927). The stands close to the Columbia River in Klickitat County are downstream of Wallula Gap, which restricted floodwaters and caused water to back up as Lake Lewis. Thus these stands were beyond the Lake. The stands in Benton County are within the Lake area. Although these plants may have invaded after the floods, this raises a question as to why invasion has not been more extensive. Any hypothesis of historic causes associated with glaciation must also account for the plants just north of Rice on the Columbia River in Stevens County, for these plants are far north of the southern terminus of at least one glacial advance.

Few plants of the Washington steppe present such a clear-cut and interesting challenge for both autecology and historic geology.

Literature Cited

Bretz, J. H., H. T. U. Smith, and G. E. Neff. 1956. Channeled scabland of Washington: New data and interpretations. Geol. Soc. Am. Bul. 67:957-1050.

Daubenmire, R. 1970. Steppe vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bul. 62.

———,and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bul. 60.

McMacken, J. G. 1927. Lake Lewis and flood-waters of Okanogan ice-sheet. Pan American Geol. 48:101-108.

Received August 18, 1980
Accepted for publication October 9, 1980

Lowell K. Nicolaus[1]

Department of Zoology
North Dakota State University
Fargo, North Dakota 58105

Todd E. Hoffman

Science Department
Butte Falls High School
Butte Falls, Oregon 97522

and

Carl R. Gustavson

Predator Control Research Laboratory
Department of Psychology
North Dakota State University
Fargo, North Dakota 58105

Taste Aversion Conditioning in Free Ranging Raccoons (Procyon lotor)

Abstract

A free ranging population of raccoons (*Procyon lotor*) were fed dead LiCl-injected chickens following a demonstrated preference for live chickens over dog food. A preference reversal was demonstrated following treatment, and the live chicken avoidance, by both identifiable and unidentifiable members of the population, continued for more than seven months.

An extensive research literature reports taste aversion conditioning to be an effective manipulation procedure for food preferences in animals (Riley and Baril 1976, Riley and Clarke 1977). At least 30 species, both vertebrate and invertebrate, have been shown sensitive to illness conditioning under laboratory conditions (Gustavson 1977). Aversive conditioning appears to be an important component in the development and maintenance of food preferences in nature (Brower 1969, Martin 1975).

Recently, taste aversion conditioning has been suggested as an alternative to killing for the control of coyote predation upon domestic livestock (Gustavson *et al.* 1974, 1976). Such an alternative, if practical, may obviate objections to predation control not only for coyotes but for skunks, raccoons, and foxes as well. Taste aversion conditioning is more humane, selective, and does not remove predators from their natural role in ecosystems.

Some opposition to the implementation of taste aversion conditioning in predator control has resulted from: (1) the inability of some researchers to produce aversions among coyotes to domestic livestock (Burns 1980, Conover *et al.* 1977, Lehner and Horn 1977, and Griffiths *et al.* 1978) when divergent procedures have been attempted;

[1]Present address: P.O. Box 395, Butte Falls, Oregon 97522

and (2) the difficulty of establishing equivalent experimental controls in field studies on aversive conditioning. No individually free-ranging predator has been observed to first prey upon domestic livestock, then feed upon baits treated with an aversion agent, and then avoid previously acceptable prey. For large wide-ranging predators, collecting such definitive field data would be difficult. However, at least one North American predator, the raccoon, may lend itself to this kind of field study.

Methods

A population containing over 20 raccoons was observed from 7 October 1978 to 13 April 1979 in Jackson County, Oregon. The study site was in a mixed conifer zone, elevation 975 m, 2.7 km from a large reservoir. The raccoons were neither hand-reared nor under restraint but had been habituated to human presence for the last 10 years by local residents feeding the raccoons approximately 600g of dog food nightly.

From 7 October 1978 to 10 November 1978 we habituated the raccoons to a new feeding site and our presence in a vehicle with lights and cameras. The feeding site was located 150 m from a residence near a conspicuous trail used by the raccoons to approach the residence. During habituation we gradually closed the distance of our vehicle to the feeting site from 40 m to 15 m. Among the raccoons observed, seven were identifiable by natural markings: Right-eye (female with two cubs, Juveniles 1 and 2), Three-leg (adult female), Right-ear (yearling), Un-female (adult female), Scar (adult of undetermined sex).

Since raccoons frequently left and returned in a single night, we could not estimate their total number. Unidentified animals were counted only while simultaneously visible. Thus, the number of unidentified individuals listed for any night was the minimum possible number.

Our initial 30 nights of observation were scheduled at random intervals to discourage anticipation of our presence. The nightly observation period extended from .5hr before sunset to .5hr after dog food was completely consumed and raccoons were no longer visible ($\overline{X} = 2.5$ hr $\pm$ .5hr). A 700g ration of dog food was present at the feeding site every night.

Live bantam chickens were tethered .5 m on opposite sides of the feeding box from 27 October to 10 November 1978. After all of the identified animals killed and/or fed on the chickens, lithium chloride-injected bantam chickens were tethered next to the box 11-14 November 1978. These baits were prepared daily. The chickens were sacrificed by cervical fracture and immediately injected with a solution of lithium chloride (82.4g LiCl/liter distilled H_2O) (Gustavson *et al.* 1976). One hundred ml of this solution was injected into a minimum of 80 different sites including subcutaneous, intraperitoneal, and intramuscular injections. Approximately 60 percent of the volume was injected into the musculature.

Baits that were not consumed in our presence were left overnight and inspected the next morning. The area within a radius of 30 m of the feed box was searched for vomitus and parts of uneaten chicken.

From 16 November to 15 December 1978 live chickens, bantams and white leghorns, were tethered and observed in the usual manner. This process was again repeated nightly from 28 March to 13 April 1979 and twice per week from 23 April 1979 through June 1979.

Results and Discussion

Prior to LiCl baiting, a mean of nine individuals per night was observed; 63 percent were identifiable. The raccoons visited the site in groups of three or more, including groups of males and yearlings without females. They defended their feeding position at the box by shouldering each other, vocalizing, and biting. They monopolized the box for 4-42 minutes ($\bar{X} = 14.3$ minutes). They did not feed from the front of the box, avoiding exposure of their backs to us. The other three sides of the box were used in an apparent random fashion while few animals were present (three or less), and evenly spaced when more were present.

The initial introduction of live chickens resulted in 15 kills between 27 October and 10 November 1978 involving all six of the identifiable animals at least once. Both Right-Eye and Three-Leg initiated kills, and their respective juveniles shared the food. Later, the juveniles attempted kills at the back or flanks followed by attacks at the head and neck. Movement or sound from the tethered chickens attracted attention, resulting in attacks and usually in kills. On three occasions chickens remaining motionless at the end of the tethers survived the night. Raccoons ate chickens preferentially to dog food.

During the LiCl baiting interval, a mean of 6.7 individuals per night was observed; 44 percent were identifiable. Three-Leg and Juvenile 1 ate baited chickens in our presence. The juvenile vomited 21 minutes after consuming approximately 200g of chicken. Morning inspection of the baits through 14 November indicated there had been substantial consumption and dismemberment in our absence. Gypsum distributed around carcasses before we left the baits overnight showed only raccoon prints. Five vomitus samples containing chicken were recovered near the feeding site during the baiting interval.

During the post-LiCl baiting interval (16 November-15 December 1978), 5.9 raccoons were observed per night; 42 percent were identifiable. None of the identifiable animals attacked the chickens during this interval and no non-identifiable individuals attacked tethered chickens, except on 9 December 1978.

After the baiting interval, the predatory behavior of both identifiable and non-identifiable raccoons changed markedly. Not only did attacks abruptly cease, but other behaviors consistent with successful aversive conditioning were noted. The raccoons avoided the sides of the feeding box where chickens were tethered. This behavior frequently resulted in a "pile-up" of raccoons behind the box, each attempting to get to the food. Sudden movements of the chickens caused the raccoons to flee, with the juveniles climbing trees. The raccoons tended to feed for shorter intervals ($\bar{X} = 8.3$ minutes), and to remove food from the box by holding it in their forepaws and moving away with tri-pedal or bi-pedal walking. The frequency of these movements before LiCl baiting was 1.6 times per animal per night, and the mean frequency after the baiting interval was 6.3 movements per animal per night. After LiCl baiting, the raccoons frequently approached the chickens in the defensive head-down attitude to about 20-40 cm, then jerked backward to take a roundabout way to the feed box ($n = 8$).

Six unidentified animals killed chickens on 9 December, as did Un-Female on 13 December 1978. These kills were made in the usual manner. The reduced visitation frequency of initially identified raccoons, and the sudden appearance of easily distinguishable but unfamiliar animals in mid-December, suggests an influx of non-averted

individuals. This observation is further substantiated by the absence of Un-Female or other animals willing to resume attacks on tethered chickens in March and April 1979.

Aversion was re-tested (28 March to 13 April 1979). During the spring test a mean of 5.8 animals was seen per night; 65 percent were the initially identified raccoons. Behavior remained as described for the post-baiting test period. Now, however, the juveniles were larger and moved more independently about the feeding site. Right-Eye and Three-Leg appeared less tolerant of their juveniles.

On two occasions, 29 March and 11 April 1979, the feeding box was moved back from the tethered chickens. Approximately 30g of iodized table salt (NaCl) was mixed in with the dog food in the box. The raccoons, including all six of the identifiable and at least six of the non-identifiable animals, fed at the sides as well as the back of the box and consumed all of the food. This particular behavior suggests that neither a "box" nor a "salt" aversion was established.

Continued weekly spot-checking of the population through June 1979, seven months after the mid-November baiting period, showed continued aversion among identifiable and most non-identifiable animals.

Predatory behavior may be grouped into two phases of activity. The first involves environmental tracking as the predator selectively scans for relevant environmental stimuli according to its current specific search image. When successful, this phase leads to the second phase: prey consumption. If consumption has high hedonic value, low risk, or low energy output, then this positive feed-back reinforces the predator's specific search image (Tinbergen 1960). If the consumptive phase is punishing, then the specific search image is suppressed and alternate prey is sought. The usefulness of taste aversion conditioning in predator control depends on the onset of illness following consumption of the prey. The resulting shift in the hedonic value of the food flavor (taste aversion) results in discontinuance of tracking, attacking, or killing the aversive prey and initiates search for alternative food sources.

If alternate foods are unavailable, aversions may be more difficult to establish. Aversive conditioning may be reduced during periods of seasonal stringency. Raccoons are omnivorous, but total availability of food items declines in the fall, possibly increasing the dependence of our raccoons on the food we provided, including chickens at the feeding site. Our results suggest, however, the established taste aversion in raccoons may have been sufficiently robust so that the seasonal fluctuations in food availability were not reflected in continued post-baiting tests. Yearlings through the weaning period of March and April and adult nursing females through May and June continued to avoid the chickens.

The chicken aversions were apparently not limited to the strain of chicken used during training. Prior to and during the baiting interval, only bantams were used, all dark brown. Aversion was tested with chickens of different breeds varying in color, size, and sex. Identification of chickens appeared to be through olfaction. The feeding site not only had live chickens but was also heavily littered with feathers from past kills. Chicken scent at the site may explain the observed decline in frequency of visitation of raccoons immediately after baiting interval.

Successful aversive conditioning of this population of raccoons under field conditions substantiates laboratory predations of Gustavson *et al.* (1979). Since the methods used were designed for aversion of canids (wolves and coyotes) and successfully

applied without major modification to Procyonids (raccoons), aversive conditioning may have application in the manipulation of food preferences for other predators.

Acknowledgment

We thank Mr. and Mrs. G. M. Nunes for their valuable help and encouragement. We also thank the Butte Falls school district, the Jackson County education service district, and Jean Pope for their assistance.

Literature Cited

Brower, L. P. 1969. Ecological Chemistry. Sci. Amer. 220: 22-29.

Burns, R. J. 1980. Evaluation of conditioned predation aversion for controlling coyote predation. J. Wildl. Manage. 41: 938-942.

Conover, M. R., J. G. Francik, and D. E. Miller. 1977. An experimental evaluation of using taste aversion to control sheep loss due to coyote predation. J. Wildl. Manage. 41: 775-779.

Griffiths, R. E., Jr., G. E. Connolly, R. J. Burns, and R. T. Sterner. 1978. Coyotes, Sheep and Lithium Chloride. Unpublished Manuscript. U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Denver, Colorado.

Gustavson, C. R. 1977. Comparative and field aspects of learned food aversions. *In* L. M. Barker, M. R. Best, and M. Domjam (Eds.). Learning Mechanisms in Food Selection, Baylor Univ. Press, Waco, Texas.

———, J. Garcia, W. G. Hankins, and K. W. Rusiniak. 1974. Coyote predation control by aversive conditioning. Science 184: 581-583.

———, D. J. Kelly, M. Sweeney, and J. Garcia. 1976. Prey lithium aversion I: Coyotes and volves. Behav. biol. 17: 61-72.

———. 1979. A preview of taste aversion coyote (*Canis latrans*) control. Paper presented at the Portland Wolf Symposium, August, 1979.

Lehner, P. N., and S. W. Horn. 1977. Effectiveness of Physiological Aversive Agents in Suppressing Predation on Rabbits and Domestic Sheep by Coyotes. Final Research Report. U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Denver, Colorado.

Martin, L. 1975. Tough and cuddly. Internat. Wildlif. 5: 14-18.

Riley, A. L., and L. L. Baril. 1976. Conditioned taste aversions: A bibliography. Anim. Learn. and Behavior. 4: 1S-13S.

———, and C. M. Clarke. 1977. Conditioned taste aversion: A bibliography. *In* L. M. Barker, M. R. Best, and M. Dobjam (Eds.) Learning Mechanisms in Food Selection. Baylor Univ. Press, Waco, Texas.

Tinbergen, L., 1960. The natural control of insects in pinewoods: I, factors influencing the intensity of predation by song birds. Archives Neerlandaises De Zoologie, Leydig 13: 265-336.

Received August 18, 1980
Accepted for publication November 9, 1980

J. L. Smith
E. J. Owens
and
B. L. McNeal
Department of Agronomy and Soils
Washington State University
Pullman, Washington 99164

Effects of Volcanic Ash on Soil Nitrogen Mineralization and Accompanying CO_2 Production[1]

Abstract

For four dominant agricultural soils from eastern Washington, treatment with moderate to heavy applications of ash from the 18 May 1980 eruption of Mt. St. Helens resulted in a slight decrease in microbial activity as evidenced by CO_2 evolution, but in little change in the amount of inorganic N produced during a standardized 28-day incubation. The effects are of insufficient magnitude to affect crop production or the nitrogen levels of groundwaters in the region.

Introduction

Crops in eastern Washington typically obtain one-third to one-half of their annual nitrogen needs from the mineralization of organic soil reserves (Leggett 1959). The eruption of Mt. St. Helens on 18 May 1980 covered much of eastern Washington's prime agricultural land with a layer of volcanic ash. Analysis of the ash has demonstrated relatively high levels of soluble salts (Fruchter *et al.* 1980, Table 5) which have previously been shown to affect nitrogen mineralization in soils (Agarwal *et al.* 1971, Broadbent and Nakashima 1971, Heilman 1975). In addition, ash constituents such as toxic metals may adversely impact soil microbial transformations.

Addition of nitrogen-free inorganic salts to soils generally results in increased inorganic nitrogen production (Agarwal *et al.* 1971, Broadbent and Nakashima 1971, Heilman 1975). The mechanisms responsible for the increase are not well understood nor agreed upon. Salts do not appear to increase microbial respiration (Agarwal *et al.* 1971). Nitrification has generally been inhibited concurrently, although the increase in ammonium levels is usually much greater than the corresponding decrease in nitrate levels (Agarwal *et al.* 1971).

The volcanic ash that extensively covered eastern Washington croplands may have created a salt effect similar to that in the laboratory experiments described above. The purpose of this study was to determine the effects of volcanic ash additions on soil nitrogen mineralization and microbial activity.

Methods and Materials

Four benchmark soils typifying several hundred thousand hectares of eastern Wash-

[1]Scientific Paper No. 5807, College of Agriculture Research Center, Washington State University, Pullman, Washington 99164. Project 0382.

ington cropland were used in this study. Since bulk samples of these soils had been obtained three weeks prior to the eruption of Mt. St. Helens on 18 May 1980, they did not include ash. Selected properties of the soils are listed in Table 1.

TABLE 1. Selected properties of the soils studied.

Soil Series	Classification	pH	Inorganic N[a]	Total N	Organic Matter
			ppm		%
Ritzville	Calcicorthidic Haploxeroll	6.5	9.7	625	1.5
Palouse	Pachic Ultic Haploxeroll	6.2	8.8	1405	3.2
Shano	Xerollic Camborthid	7.1	3.1	585	0.8
Warden	Xerollic Camborthid	6.8	41.7	649	1.8

[a]$NO_3^- + NH_4^+$

Each soil was sampled to a depth of 15 cm, placed in an airtight plastic bag, and frozen until subsequent usage. The ash used in the study was a composite sample collected from the ashfall at Pullman, Whitman Co., Washington. Average chemical analysis of samples collected statewide is shown in Table 2 (Fruchter *et al.* 1980).

TABLE 2. Average chemical properties of volcanic ash from the 18 May 1980 eruption of Mt. St. Helens (Fruchter et al. 1980).

Total Analysis	(%)	Total Analysis	(%)
SiO_2	65.0	MgO	2.2
Al_2O_3	16.9	K_2O	1.5
Fe_2O_3	4.8	TiO_2	0.7
CaO	4.9	P_2O_5	0.4
Na_2O	4.6	MnO	0.1
Water-Soluble Constituents (at 1:1 water content)			
	(mg/1, range)		(mg/1, range)
Cl^-	100-330	Na^+	81-340
NO_3^-	0-51	Mg^{2+}	11-65
SO_4^{2-}	260-1200	K^+	20-66
NH_4^+	3.3-18	Ca^{2+}	85-580
pH (1:1)	5.7-6.9	EC (mmho/cm), 1:1[a]	1.0-4.1
		50% H_2O content[b]	1.9-8.1

[a]Calculated as Σ cations (meq/liter) ÷ 10.

[b]To approximate saturation extract values.

After air drying the frozen soil for 24 hrs, 15 g subsamples were placed in 125 ml erlenmeyer flasks. Moisture content was determined by oven drying a separate subsample. Sufficient ash to provide the equivalent of 0, 45, 90, 134, 224, or 448 mt ash/ha-15 cm of field soil was mixed with the soil in each flask. Water was added to provide a moisture content of 30 percent by weight, and each resultant mixture was distributed with a spatula around the periphery of the flask bottom. Four milliliters of 1N KOH were placed in a small cup which was then placed in the bottom of each flask to trap the CO_2 evolved. Flasks were stoppered and incubated at 25° ± 0.5°C for 7, 14, 21, or 28 days. Every 3 days flasks were aerated by removing the stoppers for 10 minutes. A second set of flasks, without CO_2 traps, were used to monitor soil pH.

All CO_2 traps were analyzed weekly by transferring trap contents to a 125 ml erlenmeyer flask, adding 10 ml 1 N $BaCl_2$ and titrating with standardized HCl to the phenolphthalein endpoint. The CO_2 traps were then refilled with the flasks re-

incubated. The CO_2 evolved during successive time periods was summed to give cumulative CO_2 evolved for each treatment.

At weekly intervals one flask from each treatment (0, 45, 90, 134, 224, or 448 mt ash/ha) was extracted by shaking with 50 ml of 2 N KCl for 45 minutes. Extracts were then filtered and analyzed for NH_4^+ and NO_3^- using a steam distillation procedure (Bremner 1965). pH values for the second set of flasks were measured using a 1:1 (w:v) soil:water suspension, following a 30-minute equilibration period.

Results and Discussion

The effect of incorporated ash on microbial activity can be estimated from the CO_2-evolution data (Table 3a). Evolution of CO_2 generally decreased with increasing rates of ash application, with the lowest CO_2 evolution (least microbial activity) usually associated with samples amended with 224 or 448 mt ash/ha. Control samples of Palouse soil from Whitman Co. evolved less CO_2 than treatments receiving intermediate rates of ash application, though the lowest rates of CO_2 evolution still corresponded to the highest rates of ash amendment. Such trends may be related to the high organic matter content of the Palouse soil. Rates of CO_2 evolution were consistently, and often dramatically, lower for the 14 to 21 day interval. The reason for this phenomenon is unknown, for microbial activity had increased once more by the 21 to 28 day interval. The trend may be related to cyclic senescence of sample biomass (Knapp 1980).

The heterotropic organisms responsible for CO_2 evolution are also largely respon-

TABLE 3. Trends over time for cumulative CO_2 evolution, inorganic N release, and pH of ash-amended soils.

Soil	Rate of ash addition	(a) Days of incubation 7	14	21	28	(b) Days of incubation 7	14	21	28
	(mt/ha)	CO_2 evolved (mg-C/100g soil)				Inorganic-N release (ppm)			
Palouse	0	7.0	9.8	10.8	14.6	5.6	16.2	19.9	25.3
	45	7.7	10.6	11.6	16.4	5.0	16.8	18.8	21.9
	90	7.5	10.2	10.7	16.5	7.7	17.7	18.5	20.5
	134	8.8	11.2	11.7	16.5	7.8	16.9	19.2	19.9
	224	5.5	8.6	9.4	12.2	4.9	17.0	18.5	22.5
	448	5.6	8.8	9.8	12.6	6.9	18.4	18.9	20.2
Warden	0	15.2	25.9	30.7	40.9	37.9	52.9	37.8	25.2
	45	12.9	20.9	25.7	32.5	37.1	50.2	46.0	40.1
	90	15.4	24.2	29.0	35.7	36.5	52.5	41.7	38.5
	134	13.6	22.4	27.4	34.5	41.2	38.5	47.9	48.4
	224	13.9	23.1	28.1	34.6	46.2	44.7	53.8	59.7
	448	13.2	20.5	25.9	31.7	45.7	40.0	50.1	59.2
Ritzville	0	5.0	10.6	13.9	16.8	4.3	6.0	7.5	10.2
	45	5.2	9.9	12.4	15.1	3.4	7.0	7.5	12.2
	90	5.0	9.4	11.5	13.8	5.8	6.3	9.4	11.9
	134	5.0	9.4	11.5	14.0	4.7	7.0	9.7	12.2
	224	4.4	8.2	10.1	12.4	3.8	6.5	10.0	11.8
	448	4.0	8.3	9.7	11.6	3.8	5.5	13.5	14.3
Shano	0	4.2	7.8	9.3	11.2	4.8	5.9	9.0	11.1
	45	4.2	7.1	8.5	10.0	4.8	6.6	9.4	12.3
	90	4.0	6.9	8.4	9.9	4.4	5.8	9.1	11.6
	134	3.4	6.8	8.4	10.3	4.6	6.9	8.8	10.6
	224	3.0	6.4	7.6	8.9	4.9	5.1	9.8	10.9
	448	3.1	5.5	6.4	7.5	3.5	4.3	7.4	9.8

sible for the mineralization of organic nitrogen; therefore, lower rates of CO_2 evolution normally would be associated with lower rates of inorganic nitrogen production. Data in Table 3b show many deviations from this anticipated trend, however. The Warden, Ritzville, and Shano soils, for example, produced more inorganic nitrogen in 28 days in the presence of added ash. Paradoxically, the Palouse soil control produced a greater amount of nitrogen than several of the ash-treated Palouse samples, despite an opposite trend with respect to CO_2 production.

Since nitrification (conversion of NH_4^+ to NO_3^-, with concurrent release of H^+) tends to lower soil pH, the effect of volcanic ash additions on soil pH were examined (Table 4). The largest ash-associated change in pH after 28 days of incubation was a further decrease of 0.4 units for the Ritzville soil at the 448 mt/ha ash application rate. Ash-associated changes in pH did not continue over time. Lowering of soil pH can both solubilize organic matter and adversely affect soil microbial populations. Lower pH is particularly inhibitory to the nitrification process. With the relatively small changes in pH observed in this study we do not consider the possibilities of adverse pH changes following ash incorporation to be particularly great. The major pH change for the Warden, Ritzville, and Shano soils occurred in the first seven days of incubation, with subsequent changes inconsistent and of considerably smaller magnitude. Only for the Palouse soil, with its large organic matter content, did the pH continue to decrease with time. Furthermore, the magnitude of the pH decrease for this soil appeared to be independent of the rate of ash addition.

Data such as those of Tables 3a and 3b are difficult to interpret precisely because

TABLE 4. Electrical conductivity, and pH trends over time, for ash-amended soils.

Soil	Rate of ash addition	Electrical conductivity[a]	Days of incubation 0	7	14	21	28
	(mt/ha)	μmhos/cm			pH		
Palouse	0	303	6.20	5.70	5.70	5.70	5.60
	45	354	6.10	5.75	5.60	5.55	5.42
	90	394	6.00	5.80	5.60	5.51	5.45
	134	465	5.95	5.85	5.60	5.50	5.46
	224	586	5.90	5.70	5.57	5.49	5.41
	448	909	5.90	5.60	5.50	5.45	5.34
Warden	0	646	6.80	6.30	6.35	6.22	6.22
	45	646	6.70	6.20	6.20	6.40	6.35
	90	646	6.70	6.40	6.20	6.15	6.40
	134	788	6.70	6.00	6.08	6.15	6.12
	224	909	6.65	6.00	6.14	6.07	5.98
	448	1192	6.60	6.00	6.05	6.10	6.05
Ritzville	0	244	6.55	6.00	6.10	6.50	6.30
	45	364	6.55	6.15	6.13	6.18	6.32
	90	384	6.55	6.15	6.10	6.15	6.30
	134	450	6.50	6.10	6.15	6.02	6.10
	224	586	6.40	6.00	6.09	5.98	6.05
	448	929	5.80	5.95	6.09	5.97	5.90
Sano	0	263	7.15	6.70	6.65	6.65	6.50
	45	313	7.00	6.30	6.60	6.51	6.40
	90	388	7.05	6.30	6.50	6.51	6.40
	134	422	7.10	6.40	6.30	6.49	6.40
	224	513	7.10	6.40	6.40	6.40	6.31
	448	879	7.10	6.42	6.28	6.30	6.23

[a]E.C. measured on 1:1 (w:v) soil:H_2O basis.

of the numerous concurrent transformations which occur in incubated samples. For example, the Warden soil evidenced its peak inorganic nitrogen content at 14 days for the 0 to 90 mt/ha treatments, whereas values for the 134 to 448 mt/ha treatments continued to increase over the entire 28-day period. The latter values were also considerably greater than the former. Until this effect diminishes, there could be an increase level of inorganic nitrogen available for crop growth in the Warden soil. The first three treatments (control, 45 mt/ha and 90 mt/ha) for the Warden soil appeared to actually be immobilizing inorganic-N after 14 days, even though the 134, 224, and 448 mt/ha treatments still evidenced net mineralization during the entire period of study.

There was relatively little difference between control and treatment samples with respect to CO_2 evolved or inorganic-N produced for the Palouse, Ritzville, or Shano soils (Tables 3a and 3b). The amounts of soluble salt added in the volcanic ash (Table 2), even at the 224 or 448 mt/ha rates, did not appear sufficient for production of a stimulatory salt effect. The stimulatory effect could be somewhat masked, however, by moisture tension effects or by the presence of other constituents in the ash (such as trace metals) which might be mildly toxic to soil microbial populations. Such an interaction is suggested by the opposite effects observed with respect to CO_2 production and nitrogen mineralization rates.

Conclusions

For four dominant agricultural soils from eastern Washington, treatment with moderate to heavy applications of ash from the 18 May 1980 eruption of Mt. St. Helens resulted in a slight decrease in microbial activity, as evidenced by CO_2 evolution. For three of the four soils, there was little change in the amount of inorganic N produced during a 28-day incubation, suggesting that there should be no change in either plant-available nitrogen or in runoff or leaching of nitrogen as a result of ash incorporation. An increase in plant-available nitrogen following ash incorporation appears probable for crops grown on the Warden soil, possibly due to microbial stimulation when the salt present in volcanic ash is superimposed on already-elevated native levels of salinity. Ash incorporation initially lowered soil pH by 0.2 to 0.4 units at the 224 to 448 mt/ha rates, but no consistent changes in pH were evident over time. While effects of the ash on dominant agricultural soils from eastern Washington are generally consistent (decreased CO_2 evolution, unaffected or slightly affected N mineralization, decreased pH), these effects are of insufficient magnitude to affect crop production or the nitrogen levels of groundwaters in the region.

Literature Cited

Agarwal, A. S., B. R. Singh, and Y. Kanehiro. 1971. Ionic effects of salts on mineral nitrogen release in an allophanic soil. Soil Sci. Soc. Amer. Proc. 35:454-457.

Bremner, J. M. 1965. Inorganic forms of nitrogen. *In* C. A. Black (ed.). Methods of Soil Analysis. Part 2. Agronomy 9:1179-1237. Amer. Soc. of Agronomy, Madison, Wisc.

Broadbent, F. E., and T. Nakashima. 1971. Effect of added salts on nitrogen mineralization in three California soils. Soil Sci. Soc. Amer. Proc. 35:457-460.

Fruchter, J. S., and 21 others. 1980. Mount St. Helens ash from the 18 May 1980 eruption: chemical, physical, mineralogical, and biological properties. Science 209:1116-1125.

Heilman, P. 1975. Effects of added salts on nitrogen release and nitrate levels in forest soils of the Washington coastal area. Soil Sci. Soc. Amer. Proc. 39:7781782.

Knapp, R. B. 1980. The interrelations of carbon, nitrogen and microbal biomass during the decomposition of wheat straw. Ph.D. thesis, Washington State Univ., Pullman.
Leggett, G. E. 1959. Relationships between wheat yield, available moisture, and available nitrogen in eastern Washington dryland areas. Washington Agric. Expt. Sta. Bull. 609.
Singh, B. R., A. S. Agarwal, and Y. Kanehiro. 1969. Effect of chloride salts on ammonium nitrogen release in two Hawaiian soils. Soil Sci. Soc. Amer. Proc. 33:557-560.

Received December 16, 1980
Accepted for publication March 6, 1981

Robert A. Gresbrink
and
David D. Hopkins[1]
Biology Section
Office of Environmental Health Services
Oregon State Health Division
P.O. Box 231
Portland, Oregon 97201

Siphonaptera: Host Records from Crater Lake National Park, Oregon

Abstract

Small mammals were routinely trapped and their ectoparasites collected over a twenty year period at Crater Lake National Park, Oregon. Over 600 mammals representing 18 taxa were examined yielding 23 taxa of fleas. Flea-host records and sex ratios are presented. Male *Eutamias amoenus* were found to be infested significantly more often than females.

Introduction

Since 1960 the Oregon State Health Division Biology Section has trapped and collected ectoparasites from small mammals at Crater Lake National Park, Klamath Co., Oregon, as part of a statewide surveillance program for vector-borne disease. Noteworthy flea-host records gathered between 1960-1979 are presented herein.

Study Area Description

Elevation of the park above mean sea level is about 1340-2720 m. Several floristic zones are present; at lower elevations Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and ponderosa pine (*Pinus ponderosa*) predominate. Lodgepole pine (*Pinus contorta*) and western white pine (*Pinus monticola*) are common at middle elevations. Above this zone, mountain hemlock (*Tsuga mertensiana*), Shasta red fir (*Abies magnifica* var. *shastensis*), and noble fir (*Abies procera*) are characteristic. Whitebark pine (*Pinus albicaulis*) is common on the rocky crests encircling the caldera in which Crater Lake lies.

Methods and Materials

Small mammals were periodically collected throughout the park between July and September inclusive for the years 1960-1963, 1965, 1967, 1969, 1971, 1973, and 1977-1979. Most trap stations were between 1830 and 2130 m in elevation. Both Sherman live-traps (7.62 x 8.89 x 22.86 cm) and Museum Special traps were used. Each captured animal was individually anesthetized with diethyl ether, bled (1973, 1977-1979), and thoroughly combed for fleas which were stored in a 2 percent saline solu-

[1]Present address: 255 SW Harrison-3A, Portland, Oregon 97201.

tion. Fleas were subsequently identified by personnel at the Center for Disease Control, Vector-borne Disease Division, Plague Branch, Fort Collins, Colorado.

Results and Discussion

A total of 616 mammals representing 18 taxa were collected and yielded 23 taxa of fleas. Several mammals recorded in low numbers yielded no fleas. These are: *Sorex vagrans* (5 individuals), *Sorex palustris* (1), *Sorex* sp. (1), *Tamiasciurus douglassi* (1), *Phenacomus intermedius* (1), and *Microtus montanus* (2). The occurrence of flea species and associated mammalian hosts is shown in Table 1.

The sex ratios of the four host species captured in the largest numbers are: *Eutamias amoenus* (sex recorded in 110 individuals), 1 male: 1.1 females; *Eutamias townsendii* (28), 1:0.6; *Spermophilus lateralis* (236), 1:1.2; *Peromyscus maniculatus* (125), 1:0.8. Chi-square was used to test for differences in the rate of infestation associated with host sex (Table 2). No significant correlation was found except that in *E. amoenus* ($p < 0.001$, $df = 1$), 66.7 percent of all males were infested compared to 26.8 percent of the females.

Information regarding flea sex ratios is incomplete because the sex of individual fleas was not recorded during 1965 and 1969-1973. However, data from the remaining years regarding the two predominant species indicate a sex ratio of about 1:1.4 for both *Oropsylla idahoensis* (56 males, 81 females) and *Monopsyllus eumolpi* (57, 79).

Accidental infestations were recorded from several hosts. The following references to preferred hosts were drawn from Hubbard (1947). *Orchopeas sexdentatus*, commonly found on *Neotoma* spp., was recovered from one *Clethrionomys occidentalis*. Eight *Oropsylla idahoensis* were removed from *Eutamias* spp., *Peromyscus maniculatus*, and *C. occidentalis*. The preferred hosts of *O. idahoensis* are *Spermophilus* spp.; at Crater Lake they clearly exhibited a host preference for *S. lateralis*, readily parasitizing both sexes. *Foxella ignota*, a flea of *Thomomys* spp., was recorded from *Neotoma cinerea*. *Eutamias amoenus, Spermophilus lateralis*, and *Microtus* sp. were host to *Monopsyllus wagneri*, commonly found on *P. maniculatus*. A true *Scapanus* flea, *Nearctopsylla jordani* was taken from *P. maniculatus*. *Monopsyllus cilliatus*, a flea of *Eutamias* spp., was recovered from *S. lateralis, P. maniculatus*, and *Martes americana*, a chipmunk predator.

Hubbard indicates that *Onychomys leucogaster* is probably the true host of *Monopsyllus exilis* and that the flea would be found wherever *O. leucogaster* occurs. Two *M. exilis* were taken from *P. maniculatus* at Crater Lake, outside the range of *O. leucogaster*.

Catallagia sculleni is primarily a *P. maniculatus* flea. In this study it was recovered from *Eutamias* spp., microtines, and *Zapus trinotatus*. In the Pacific Northwest, Hubbard recovered only *Megabothris abantis* and *M. quirni* on *Z. trinotatus*.

Hubbard reports that *Opisodasys keeni* is the second most common flea on *P. maniculatus* and is found west of the eastern base of the Cascade Range; only one was recovered at Crater Lake. Perhaps the scarcity of *O. kenni* is due to the proximity of the study site to the eastern terminus of the species' range.

TABLE 1. Occurrence of flea species on mammals from Crater Lake National Park, Oregon, 1960-1979.

Species	Number collected	Number infested	Orchopeas sexdentatus Baker	Opisodasys keeni (Baker)	Thrassis sp.	Oropsylla idahoensis (Baker)	Foxella ignota (Baker)	Malaraeus telchinum (Rothschild)	Malaraeus bitterootensis (Dunn)	Malaraeus sp.	Megabothris abantis (Rothschild)	Monopsyllus wagneri (Baker)	Monopsyllus ciliatus (Baker)	Monopsyllus enmolpi (Rothschild)	Monopsyllus exilis (Jordan)	Monopsyllus sp.	Atyphloceras sp.	Catallagia sculleni Hubbard	Catallagia chamberlini Hubbard	Catallagia sp.	Peromyscopsylla hespheromys (Baker)	Peromyscopsylla selensis (Rothschild)	Peromyscopsylla sp.	Hystricopsylla occidentalis Holland	Nearctopsylla jordani Hubbard
Ochotona princeps	2	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eutamias amoenus	110	51	—	—	1	4	—	—	—	—	—	1	32	73	—	—	—	—	—	4	—	—	—	—	—
Eutamias townsendii	31	11	—	—	—	1	—	—	—	—	—	—	16	5	—	2	—	4	—	1	—	—	—	—	—
Eutamias sp.	51	21	—	—	—	1	—	—	—	—	—	—	1	78	—	—	1	1	—	—	—	—	1	—	—
Spermophilus lateralis	236	158	—	—	—	329	—	—	—	—	—	2	3	3	—	—	—	—	—	1	—	—	—	—	—
Peromyscus maniculatus	126	64	—	2	—	1	—	1	—	—	1	57	2	—	2	—	—	—	—	7	12	1	7	1	1
Neotoma cinerea	2	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Clethrionomys occidentalis	23	10	1	—	—	1	—	4	—	2	—	—	—	—	—	—	—	2	1	1	—	1	6	—	—
Microtus richardsoni	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Microtus sp.	13	4	—	—	—	—	—	1	—	—	18	1	—	—	—	—	—	2	—	3	—	—	—	—	—
Zapus trinotatus	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Martes americana	1	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Total	616*	324	2	2	1	337	1	6	1	2	19	61	55	159	2	2	1	10	1	17	12	3	14	1	1

*Included are the 11 indivduals (five species) described in the text from which no fleas were recovered.

TABLE 2. Distribution by host sex of fleas on four common mammals at Crater Lake National Park.

Species	Absent		Present	
	Male	Female	Male	Female
Eutamias amoenus	18	41	36	15
Eutamias townsendii	11	6	6	5
Spermophilus lateralis	38	40	70	88
Peromyscus maniculatus	34	28	36	27

Acknowledgments

We gratefully acknowledge the flea identifications made by the following Center for Disease Control personnel: E. G. Campos, R. B. Eads, G. O. Maupin, F. M. Prince, and H. E. Stark. We further wish to thank the Crater Lake National Park personnel for their assistance and cooperation, and R. B. Forbes for reviewing the manuscript.

Literature Cited

Hubbard, C. A. 1947. Fleas of Western North America. Iowa State Univ. Press. Ames.

Received August 15, 1980
Accepted for publication September 15, 1980

Kern Ewing

Botany Department, AJ-10
University of Washington
Seattle, Washington 98195

A Comparison of Treeless Areas in the Forested Foothills of the Cascade Mountains of Western Washington

Abstract

Eighteen tree-free sites within closed forest in the Cascade foothills of western Washington were compared for species composition and cover values. The use of information gain as a dissimilarity measure allowed the sites to be classified into five major habitats by an agglomerative polythetic technique: 1) tuff breccia outcrops, 2) talus slopes, 3) cliff faces, 4) sites in areas of recent disturbance, and 5) sites in areas of well-developed soils. Nine characteristics, which could be determined for the 105 plant species enumerated and which showed variation, were used to compare adaptive trends observed on the sites within each habitat type. Habitat 4, disturbed sites, had the most pronounced differences in adaptive trends among the five types. Habitats 1, 2, and 3—the shallow-soil, rocky sites—were quite similar in the characteristics used for comparison. Habitat 5, on well-developed soils, was similar to Habitats 1, 2, and 3 when *Rubus* species and ferns were not considered. Tuff breccia outcrops, the most prominent tree-free sites in the area, supported few plants with unique adaptations for outcrop existence and no endemics. Cycles of fire and erosion and the attendant loss of soil are proposed as the reason for existence of the rocky sites as treeless areas.

Introduction

Treeless outcrops in forested areas of the United States have been studied extensively, and their existence has been attributed to a combination of factors. These include thin soils, resistant bedrock, exposed sites, harsh microclimatic conditions, and continuous or catastrophic disturbances. Outcrops are generally thought to be in a state of suspended or slowed succession in which soil formation is the most important factor controlling the development of plant cover. The speed or success of advancement from early to later seral states is thought to depend first upon the establishment of lichens, mosses, or small vascular plants on bare rock or in microsites. Geomorphic factors controlling this establishment include slope, aspect, crevices or depressions to catch soil and water, nature of parent rock, and presence of soil and water sources upslope. Succession may be repeatedly set back by catastrophic events such as windthrow, sloughing of soil, vegetation on steep slopes, and fires.

The phenomenon of treeless outcrops has been studied extensively in the southeastern United States where they are conspicuous, and also in other forest and woodland zones. Whitehouse (1933) dealt with succession on Enchanted Rock, a large granite outcrop in Texas. In the southern Appalachians, Harper (1939) observed granite outcrops in Alabama; Oosting and Anderson (1937, 1939) reported on granite rocks and cliffs in North Carolina; Keever *et al.* (1951) studied granite outcrops in North Carolina; McVaugh (1943) investigated low elevation flat rocks which cover extensive areas in South Carolina; Burbanck and Platt (1964) studied granite outcrops in Georgia. Sharitz and McCormick (1973) studied granite outcrops in Georgia and North Carolina. Platt (1951) worked in mid-Appalachian shale barrens. In the Mid-

west, Winterringer and Vestal (1956) investigated the bare areas atop cliffs. In Idaho, Daubenmire and Slipp (1943) studied succession on talus slopes. In Montana, McCune (1977) inferred succession on talus from cover status of vegetation.

Anomalous areas of rock outcrops exist in lower elevation *Tsuga heterophylla-Pseudotsuga menziesii* forests of western Washington. In this area the seasonal pattern of precipitation, considered by some to be an important factor in soil loss, is the reverse of that in the Southeast. The Appalachian mountains and the Midwest have heavy summer rains. In western Washington, there is very little summer rain; summer drought is common. At the site of this study (Rattlesnake Mountain, near Cedar Falls, Washington, Fig. 1) annual precipitation is 2270 mm, 90 percent of which is fairly evenly distributed in the fall and winter, mostly as rain. Torrential downpours are unusual. In the Southeast and Midwest, catastrophic setbacks in succession may be caused by windthrow during storms, at a time when the thin layer of soil supporting the vegetation is soft and weakened. In the Northwest, windstorms are not generally so violent. Outcrops in the Northwest suffer setbacks in succession caused by slumping of layers of soil and vegetation on slopes when saturated, but the phenomenon was not often observed in this study. Soil building has been reported to be extremely slow or regularly reversed in the Midwest and Southwest, whereas the development due to cryptogam growth and heavy peripheral litter accumulation from the coniferous forest in the Northwest is fairly rapid. The outcrops studied in this investigation and similar more shaded areas nearby appear to be proceeding rapidly to more advanced stages of succession toward closed forest.

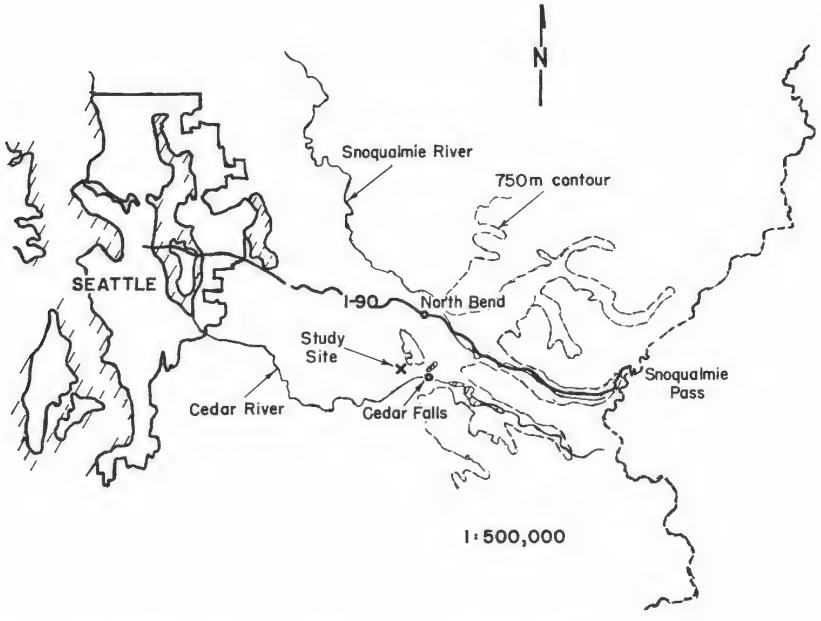


Figure 1. Location map of the study site near Cedar Falls, Washington.

Methods

Tree-free sites within second growth forest were located in an area roughly 2000 x 1200 m at 290-590 m elevation. Tree-free sites were classified as belonging to any one of five major habitat types: 1) tuff breccia outcrops, 2) talus slopes, 3) cliff faces, 4) sites of recent disturbance such as roadbeds, cutbanks, gravel pits, and unstable portions of talus slopes, and 5) sites with well-developed soils such as old fields and forest clearcuts. The response of vegetation to the sites was compared in order to gauge plant perception of the sites as habitats based on previously described ecological affinities of the species.

Eighteen study sites were located in the valley of the Cedar River. Except for two forested sites established to determine understory vegetation composition, all sites lacked tree cover. All were on south-facing slopes. At each site, species presence and cover data were collected using 1 m^2 sample quadrats randomly placed, with 12 to 20 quadrats along two to three transects per site. Quadrat data were recorded until cover values for all but the rarest of species at each site were obtained. Nomenclature follows Hitchcock *et al.* (1955, 1959, 1961, 1964, 1967) for vascular plants and Lawton (1971) for bryophytes. Sampling was accomplished during the summers of 1977 and 1978.

Cover data for the 105 species from 20 sites were arranged in a matrix. Using ORDIFLEX (Gauch 1977), the matrix was log-transformed in order to emphasize the floristic relationships of the sites and to minimize the contribution of mat-forming cryptogams. This procedure seemed desirable because of the low cover values for flowering plants at outcrop sites and the higher cover values for flowering plants found on deeper soils (Ewing 1978). Classification of sites was accomplished using the MINFO clustering program (Goldstein and Grigal 1971). MINFO is an agglomerative polythetic method which uses information gain as a dissimilarity measure. The product of MINFO allows a classification dendrogram to be constructed.

Five habitat groups of stands or sites were established using MINFO. The first habitat, designated as "tuff breccia outcrops," was composed of weathered rock on 60-90 percent slopes. Thirty-five plant species were found in this group, but it was dominated by mat-forming cryptogams which had cover values generally higher than 85 percent. Cryptogams, perennial graminoids, composites, ferns, small shrubs, and a number of diminutive annuals characterize the vegetation. The dominant species for each habitat type are listed in Table 1. In the second habitat, "talus slopes," approximately the same kinds of plant associations occurred, but only 29 species were present. *Acer circinatum* and *Ribes sanguineum*, whose seedlings root between talus blocks, were found in small numbers. The third group, and the last of the shallow-soil outcrop habitats, was designated "cliff faces." Because of the partial shading at some cliff face sites, the proportion of epilithic ferns was greater than at the other rocky sites. In addition, the cliff faces offer a wider range of microhabitats and support forest floor species as well as several species found on disturbed sites; 35 species were found. The fourth habitat was called "sites in areas of recent disturbance" and is comprised of sites which are subjected to massive and continual instability, such as the gravelly steep base of a cliff, a gravel pit, a roadbed, and road cutbanks. Of the 53 species sampled here, 30 of them, all weedy pioneers, did not occur in the outcrop habitats. The last habitat, "sites in areas of well-developed soils," occurs in an old field, a two-year-old clearcut,

and in closed forest. It supports 66 species, including those of meadows and clearings, forest edge, and forest.

In order to determine whether the communities which were found on outcrops might be distinguished by a dominant life history or by some combination of morpho-

TABLE 1. Dominant species for each habitat.

Habitat	Species	Cover value*
No. 1, Tuff Breccia Outcrops	**Rhacomitrium canescens**	9
	Polytrichum juniperinum	5
	Selaginella densa	5
	Gaultheria shallon	4
	Holodiscus discolor	3
	Danthonia spicata	2
	Holcus lanatus	2
	Hypericum perforatum	2
	Rubus ursinus	2
	Amelanchier alnifolia	1
	Berberis nervosa	1
	Festuca occidentalis	1
	Fragaria virginiana	1
No. 2, Talus Slopes	**Rhacomitrium canescens**	9
	Danthonia spicata	4
	Polytrichum juniperinum	4
	Selaginella densa	4
	Holodiscus discolor	3
	Holcus lanatus	2
	Arenaria macrophylla	1
	Berberis nervosa	1
	Festuca occidentalis	1
	Acer circinatum	1
No. 3, Cliff Faces	**Polytrichum juniperinum**	6
	Rhacomitrium canescens	6
	Polystichum munitum var. imbricans	4
	Rubus ursinus	4
	Gaultheria shallon	3
	Heuchera micrantha	2
	Holodiscus discolor	2
	Polystichum munitum var. munitum	2
	Amelanchier alnifolia	1
	Asplenium trichomanes	1
No. 4, Sites on Areas of Recent Disturbance	**Alnus rubra**	7
	Digitalis purpurea	4
	Holcus lanatus	4
	Elymus glaucus	3
	Equisetum arvense	2
	Luzula campestris	2
	Rhacomitrium canescens	2
	Rubus ursinus	2
	Sagina procumbens	2
No. 5, Sites in Areas of Well-developed soils	**Polystichum munitum var. munitum**	6
	Berberis nervosa	5
	Rubus ursinus	3
	Acer circinatum	2
	Athyrium filix-femina	2
	Cirsium arvense	2
	Gaultheria shallon	2
	Pteridium aquilinum	2
	Digitalis purpurea	1
	Prunella vulgaris	1
	Urtica dioica	1

*Cover values are based upon percent coverage, log-transformed and expressed as a decile value, with 9 the highest value.

logical features, nine species characteristics in which variation occurred were compared. For example, the characteristic "duration" might be used to divide the 105 species observed into three groups: 1) perennials, 2) biennials, and 3) annuals. When segregation into the character states of all nine characteristics is analyzed, trends or responses to environmental conditions become clearer. The characteristics used are listed in Table 2. The state of a particular characteristic into which any species might be placed was determined from the literature, primarily Hitchcock *et al.* (1955-1967).

TABLE 2. Species characteristics.

Characteristic	States
Duration	1. Annual, 2. Biennial, 3. Perennial
Raunkiaer Life Form	1. Non-vascular Cryptogam, 2. Nanophanerophyte, 3. Chamaephyte, 4. Hemicryptophyte, 5. Geophyte, 6. Therophyte
Wind Dispersal	1. Not wind-dispersed, 2. Wind-dispersed
Diaspore Type	1. Single or clustered seeds or spores, 2. Fruit, 3. Fruit plus floral parts or bracts, 4. No. 1 plus rooting stem or leaf or sprouting root. 5. No. 2 plus rooting stem or leaf or sprouting root, 6. Part or entire inflorescence or fruit plus floral parts, rooting stem, leaf, sprouting root
Geographic Distribution	1. Pacific Northwest, 2. Western North America, 3. United States or North America, 4. Circumboreal or cosmopolitan
Weediness (Hitchcock et al. 1955-1967)	1. Non-weedy, 2. Slightly weedy, 3. weedy or very weedy
Affinity for Rocky Sites (Hitchcock et al. 1955-1967)	1. Seldom found, 2. Found in gravelly open spaces or rocky soils, 3. High fidelity to rocky sites
Pollination Vector	1. Not a pollen-bearing plant, 2. Wind, 3. Insect, 4. Bird, 5. Bird or insect, 6. Wind or insect
Moldenke Outcrossing Categories (Moldenke 1976)	1. Genetically self-compatible, 2. Self-incompatible, 3. Apomictic, 4. Genera having species both No. 1 and No. 2, 5. Genera having species both No. 1 and No. 3

The S.P.S.S. (Statistical Package for the Social Sciences) program CROSSTABS was used to structure the data in a way which would allow investigation of 1) sets of relationships among and between the habitat groups formed from the MINFO classifications, and 2) the occurrence of certain species characteristics in a particular habitat (Nie *et al.* 1975). For each characteristic used, CROSSTABS allows a comparison to be made, between habitats, of the distribution of the states of that characteristic. CROSSTABS computes cross-tabulation or contingency tables for discrete variables. The joint frequency distributions are analyzed with the Chi-square statistic to determine whether the variables are statistically independent. The null hypothesis for contingency table testing in this case is that the frequencies of certain states of a characteristic are the same for all five habitats (Zar, 1974). In cases where the null hypothesis was rejected for the five habitats tested together, every pair of habitats was compared, and the null hypothesis that frequencies between the two habitats were the same was tested for each pairing. A Chi-square statistic greater than a $X^2_{0.05}$ critical value was required to reject the null hypothesis.

Results

Figure 2 shows matrices of habitat (tuff breccia outcrops, talus slopes, etc.) against habitat for all nine species characteristics. Using the 0.95 significance level to reject

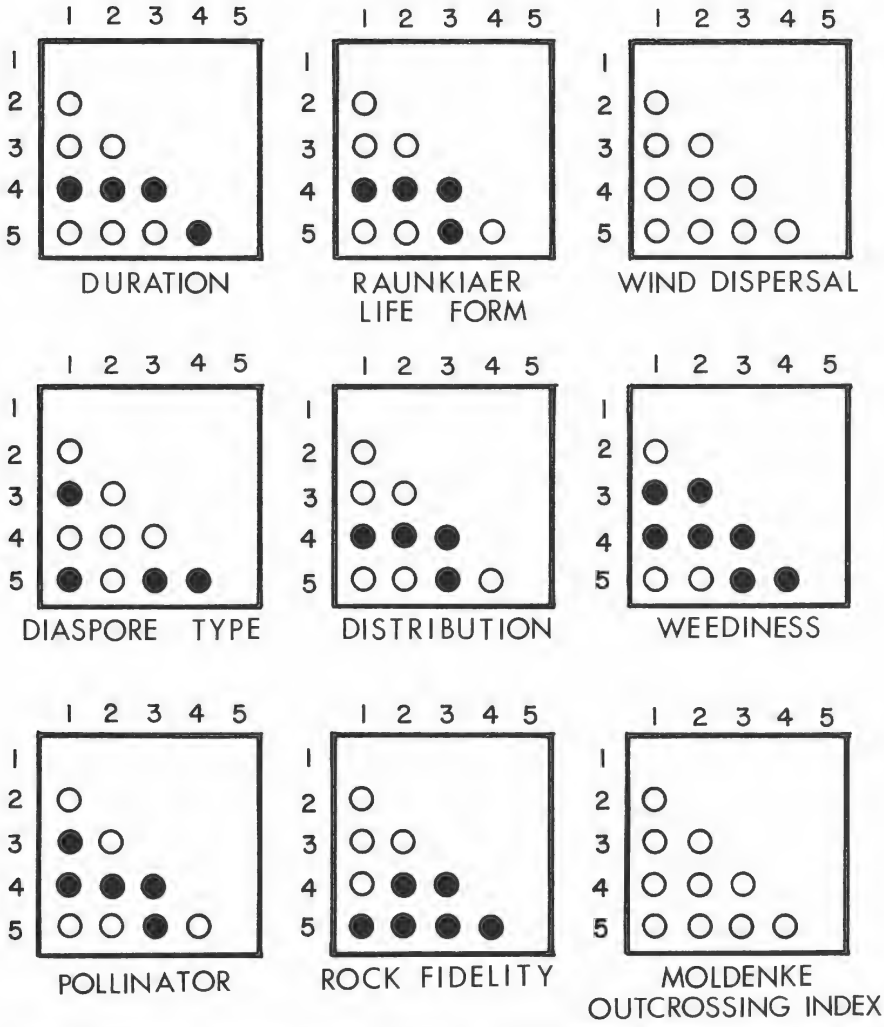


Figure 2. Significant differences between habitats ($p = .05$) for each adaptive characteristic. Lack of significant difference shown by an open circle (O); significant difference is shown by a darkened circle (●). Habitats represented on axes are: 1) Tuff breccia outcrops, 2) Talus slopes, 2) Cliff faces, 4) Sites in areas of recent disturbance, 5) Sites in areas of well-developed soils.

an hypothesis of no difference, significant differences in characteristics between habitats are indicated by a darkened circle. Variation in the distribution of species within each state of a characteristic is accounted for as follows.

Duration

Habitat 4 had a significantly greater proportion of biennials than all other groups.

Raunkiaer Life Form

Habitat 4 differed from all except No. 5. Habitat 4 had a large proportion of species

which were hemicryptophytes (mostly biennial composites) and small numbers in other categories. Habitat 3 had a higher proportion of chamaephytes (low evergreen ferns defined here as chamaephytes) and a lower proportion of hemicryptophytes than Habitat 5.

Wind Dispersal

No significant difference existed between plants that were wind-dispersed or not wind-dispersed in the five habitats.

Diaspore Type

Most of the variation can be accounted for by Habitat 5. It had a smaller proportion of plants with single or clustered seeds or spores (fewer composites and mosses) and a larger proportion of plants with fruit plus rooting stem or leaf (more *Rubus*) than all other habitats.

Geographical Distribution

Most of the variation in distribution is accounted for in Habitat 4 with its high proportion of circumboreal and cosmopolitan species and a low proportion of western North American species. Habitat 4 does not differ significantly from Habitat 5.

Weediness

All variation in weediness is generated in Habitat 4 and Habitat 3. These two groups are different from every other group and from each other. Habitat 4 has a lower percentage of non-weedy species and a higher percentage of weedy or very weedy species than any other group, and the situation is reversed in Habitat 3.

Pollination Vector

Variation in this characteristic is accounted for by Habitat 1, 3, and 4, each of which differs from two to three other habitats. Habitat 1 has a high percentage of insect-pollinated species. Habitat 3 has a high proportion of plants not bearing pollen. Habitat 4 has insect-pollinated species plus a higher percentage of wind-pollinated graminoids and a very few non-pollen bearing plants.

Affinity for Rocky Sites

All variation in this characteristic may be attributed to Habitats 4 and 5. Both have a very high proportion of plants "seldom found on rock," while Habitat 5 has few plants with "high fidelity to rocky sites."

Moldenke Outcrossing Index

No significant difference was found between sites.

A synthesis of the differences and similarities determined by crosstabulation reveals that Habitat 4 is most unlike the other habitats. Habitats 1, 2, and 3 closely resemble one another. Were it not for the occurrence of ferns in Habitat 3 and by *Rubus* and weedy species on the sites of Habitat 5, Habitat 5 would not be different from the three rocky, thin-soil habitats. The similarities between adaptations found on the rocky sites and those on the productive deep soil sites suggest that the rocky sites are more mesic than might be expected, but the plants on the outcrops are smaller.

Discussion

Colonization and succession on open tuff breccia outcrops in the Cedar Falls area appear

to proceed in a manner similar to that observed by Oosting (1948) and Keever *et al.* (1951) in the Southeast, and by Winterringer and Vestal (1956) in the Midwest. A moss pad 10-15 cm thick is found upon most of the rock sites; on sites with highly weathered and crumbling rock, the combination of a moss pad and a developing gravelly layer atop the rock allows invasion by species with vigorous rhizomatous growth from the edge of the surrounding forest. Succession on talus fans is promoted by the establishment of shrubby species in the interstitial spaces between talus blocks. Cliff faces show a succession which is featured by a shift in dominance from species found at open outcrops to a fern-dominated association as the forest canopy rises and eventually shades the cliff.

At tuff breccia outcrop sites, soil development is controlled to a great extent by aspect and by shading from adjacent forest, by the tendency of the rock to exfoliate and form a gravelly scree, and by slope angle. There is a discernible moisture gradient in the summer across the border between outcrop and forest; this border and the soil-filled pockets and crevices on the outcrops provide many microhabitats and support more higher vascular plant vegetation than the rest of the site. No unique combination of the nine characteristics used is found for comparing the species that exist on the tuff breccia sites. Species are not alike in their requirements or the way in which they colonize particular habitats or ecological niches. Winterringer and Vestal (1956) found this lack of uniqueness at outcrops, which led them to conclude that the species or combinations of species found at any particular soil lodgement depended mostly upon chance elements of dispersal and establishment. McVaugh (1943) found that the presence of endemics at flat rock sites in South Carolina was a good indication of the continual existence of bare rock at an outcrop site during recent geological periods. No endemics were found at any of the Cedar Falls sites.

Evidence for a recent origin of the open tuff breccia outcrops comes from the fire history of the Cedar River Valley. It is known that the area was logged between 1914 and 1920 and that a major fire swept down most of the valley from ridge to ridge in 1923. At two of the large open tuff breccia sites burned snags of mature forest trees were found, their roots extending off in the direction of the surrounding deeper soils. This suggests that there was a soil cover sufficient to support these trees at the outcrops either at the time of logging or at the time of the fire and that the loss of shading followed by a hot fire allowed the thin soil above the rock to be eroded by rainfall. The ephemeral nature of the tuff-breccia outcrops as tree-free areas, if indeed they are successional, may be due in no small part to the substantial, evenly distributed and gentle nature of the rainfall in this area which removes little soil and helps maintain more "mesic" substrates than would otherwise exist. Moderate temperatures and the lack of continuous snow cover in winter also create favorable conditions for rapid succession. Much erosion on southern Appalachian outcrop sites is attributed to heavy summer rains which seldom occur in the Northwest. The relatively benign nature of the climate at these sites and the low elevation, as well as the moss mat which minimizes water loss and temperature extremes in summer and winter, may allow for an accelerated succession when compared to many sites described in the literature of rock outcrops.

The following conclusions are drawn from observations and analyses of data from this study:

1. Succession in this Pacific Northwest forest outcrop habitat occurs in a way

similar to that described in the literature of the Southeast and Midwest in the United States. Reversals due to catastrophic events such as windthrow and erosion during violent summer storms are not great in the Northwest, but reversals due to fires are a definite threat. Clearcutting may have the same effect, but loss of soil might not be so great.

2. A luxuriant and deep mat of moss and *Selaginella* is an expedient in the binding and formation of soil, and many of the species found take root in this substrate, whereas most of the species which root in the rock crevices below the mat have their seedlings protected by the ameliorating presence of the mat.
3. The age of the outcrops as tree-free habitats was not established by the presence of endemics. No endemics were found.
4. The majority of species found on these outcrops are those which might be found in any successional, open habitat. Almost all seed sources are available nearby in a number of different habitats.
5. The lack of special trends of adaptive patterns in communities on outcrops may suggest that the outcrops are ephemeral.
6. Adaptations found on deep soil sites are reasonably successful on these outcrops.
7. Special adaptations which might be expected to occur on rock outcrops (i.e., succulence, evergreenness, storage roots) are absent or are found in only a few instances.
8. The encroachment of soil-binding vegetation and maturing forest trees in adjacent shallow-soil areas suggest that succession from open outcrop to closed forest will occur rapidly in the absence of catastrophic setbacks.

Acknowledgments

I thank A. R. Kruckeberg for advice and critical review of the manuscript, which is taken from a Master's thesis submitted to the Department of Botany, University of Washington.

Literature Cited

Burbanck, M., and R. B. Platt. 1964. Granite outcrop communities of the Piedmont Plateau in Georgia. Ecology 45: 292-306.

Daubenmire, R., and A. W. Slipp. 1943. Plant succession on talus slopes in northern Idaho as influenced by slope exposure. Bulletin of the Torrey Botanical Club 70: 473-480.

Ewing, K. 1978. An Analysis of Vegetation on Rock Outcrops in the Vicinity of Cedar Falls, King Co., Washington. Univ. of Washington M.S. thesis.

Gauch, H. G. 1977. ORDIFLEX. Ecology and Systematics. Cornell University, Ithaca, N.Y.

Goldstein, R. A., and D. F. Grigal. 1977. Computer Programs for the Ordination and Classification of Ecosystems. ORNL-1BD-71-10, Oak Ridge National Laboratory.

Harper, R. M. 1939. Granite outcrop vegetation in Alabama. Torreya 39: 153-159.

Hitchcock, L. C., A. Cronquist, M. Ownbey, and J. W. Thompson. 1955, 1959, 1961, 1964, 1967. Vascular Plants of the Pacific Northwest. Univ. of Washington Press, Seattle and London. 5 vols. pp. 343, 510, 597, 614, 914.

Keever, C., H. J. Oosting, and L. E. Anderson. 1951. Plant succession on exposed granite of Rocky Face Mountains, Alexander County, North Carolina. Torrey Botanical Club Bulletin 78: 401-421.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan.

McCune, B. 1977. Vegetation development on a low elevation talus slope in western Montana. Northw. Sci. 51: 198-207.

Mackin, J. M. 1941. Glacial geology of the Snoqualmie-Cedar area, Washington. Journal of Geology 49: 449-481.
McVaugh, R. 1943. The vegetation of the Granite Flat Rocks of the southeastern U.S. Ecological Monographs 13: 119-166.
Moldenke, A. 1976. California pollination ecology and vegetation types. Phytologia 34: 305-361.
Nie, N., H. Hull, J. Jenkins, K. Steinbrenner, D. Brent. 1975. Statistical Package for the Social Sciences. 2nd ed. McGraw Hill, N.Y.
Oosting, H. J., and L. E. Anderson. 1973. The vegetation of a barefaced cliff in western North Carolina. Ecology 18: 280-292.
———. 1939. Plant succession on Granite Rock in eastern North Carolina. Botanical Gazette 100: 750-768.
Platt, R. B. 1951. An ecological study of the Mid-Appalachian shale barrens and of the plants endemic to them. Ecological Monographs 21: 261-300.
Raunkiaer, C. 1937. Plant Life Forms. Clarendon Press, Oxford.
Sharitz, R. R., and J. F. McCormick. 1973. Population dynamics of two competing annual plant species. Ecology 54: 723-740.
Whitehouse, E. 1933. Plant succession on central Texas granite. Ecology 14: 391-405.
Winterringer, G. S., and A. G. Vestel. 1956. Rock ledge vegetation in southern Illinois. Ecological Monographs 26: 105-130.
Zar, J. 1974. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, N.J.

Received April 24, 1980
Accepted for publication June 22, 1981

Thomas J. Nimlos
and
Hans Zuuring
School of Forestry
University of Montana
Missoula, Montana 59812

The Distribution and Thickness of Volcanic Ash in Montana

Abstract
The distribution and thickness of volcanic ash in western Montana was determined. Ash is more common at high elevations, in the vicinity of the main lobe of deposition from the Mazama eruption, on north aspects, and on gentle slopes. In the areas of the main lobe of ash deposition it is associated with many habitat series, including *Pseudotsuga menziesii*, but at the limits of its distribution it occurs usually with the *Abies lasiocarpa* series. Prediction of ash thickness was marginally successful since only 22 percent of the total variation in thickness could be accounted for by the selected independent variables.

Introduction

The eruption of Mt. St. Helens on 18 May 1980 focused attention on the impact of volcanic ash on the Pacific Northwest, including soils formed in ash. Approximately 2 x 10^6 ha of forested land in western Montana have been covered with a layer of volcanic ash that originated from a number of volcanos in the Cascade Range (Nimlos 1980). Most of the ash in Montana came from Mt. Mazama with smaller amounts from Glacier Peak and negligible contributions from Mt. St. Helens. Soils formed in ash have properties that are of importance to forest land management; very low bulk density, high porosity, and high water transmission and retention values—to name a few (Nimlos 1981). The thicker the mantle, the more pronounced these properties.

Ash does not occur as a uniform blanket in the area of deposition but is on some land surfaces and not on others. It is found throughout western Montana, from Lost Trail Pass on the south to the Canadian border on the north and from 30 km west of Helena in the east to the Idaho border on the west. It is usually on mountain slopes, rarely in intermountain valleys.

Ash is most widespread in the northwest corner of the state in line with the main lobe of Mazama and Glacier Peak ash falls and becomes thinner to the southeast (Ottersberg 1977). The maximum ash thickness is in the Cabinet Mountains near Trout Creek, where mantles of 6 dm occur. Ash mantles less than 1 dm are not common; thin ash mantles presumably have been mixed into the underlying material or eroded.

The objective of this research was to characterize the ash distribution and predict thickness as a function of elevation, habitat types (Pfister *et al.* 1977), aspect, slope gradient, and distance from the main lobe of deposition.

Methods

Data Base

The data for this study came from 326 profile descriptions of soils formed in volcanic

ash which were written by soil scientists of the Forest Service and Soil Conservation Service. The descriptions are part of unpublished agency records for mapping unit characterization and represent typical profiles in each mapped area. They were supplied by agency soil scientists.

Volcanic ash is identified primarily by color, density, boundary, and coarse fragment content. The distribution of the profiles is shown in Table 1 by National Forest and the location of the forests in Figure 1. The full extent of the conditions associated with ash may not have been depicted completely; however, field experience suggests that most of the actual range, both geographic and levels within independent variables, have been represented. The geographical range of the profiles is thoughout western Montana, with only a few east of the Continental Divide.

TABLE 1. Number of field descriptions from National Forests in western Montana and adjacent areas.

Forest	Number of field descriptions
Kootenai	49
Flathead	112
Lolo	87
Bitterroot	13
Deer Lodge	19
Beaverhead	2
Lewis & Clark	18
Helena	6
Idaho (all forests)	20
	326

The data are represented by the following variables: elevation, habitat type (represented in some analyses by a combination of a temperature and moisture index each scaled from 0 to 10-S; Arno, Forest Service, Missoula; pers. comm.), aspect, slope gradient, and ash thickness; all data were taken from field sheets. An additional variable, the distance from an approximation of the main lobe of deposition, was established by drawing a line from Crater Lake to the northeast through the area of the main lobe (Figure 1), as illustrated by Ottersberg (1977). This line ran about 10 km southeast of Libby, Montana. Distances from the main lobe were measured at right angles to the above line, approximately in northwest and southwest directions.

Data Analysis

Distribution. A number of two-way and three-way tables were constructed to identify differences in the frequency of occurrence of ash mantles as related to various variables taken two and three at a time. In order to make meaningful interpretations from the above tables, certain assumptions had to be made. We assumed that slope gradient and aspect were uniformly represented throughout the study area but that elevation classes and habitat types were not. To test for the presence of a confounding influence of elevation on ash distribution, the difference between the observed (sampled) and expected (actual) distribution of elevation classes was determined within each of four groups based on distance from the main lobe. A random sample of 100 points was located within each distance group with a dot grid on a planimetric map of the study area. These points were then classified into four elevation intervals. To detect significant

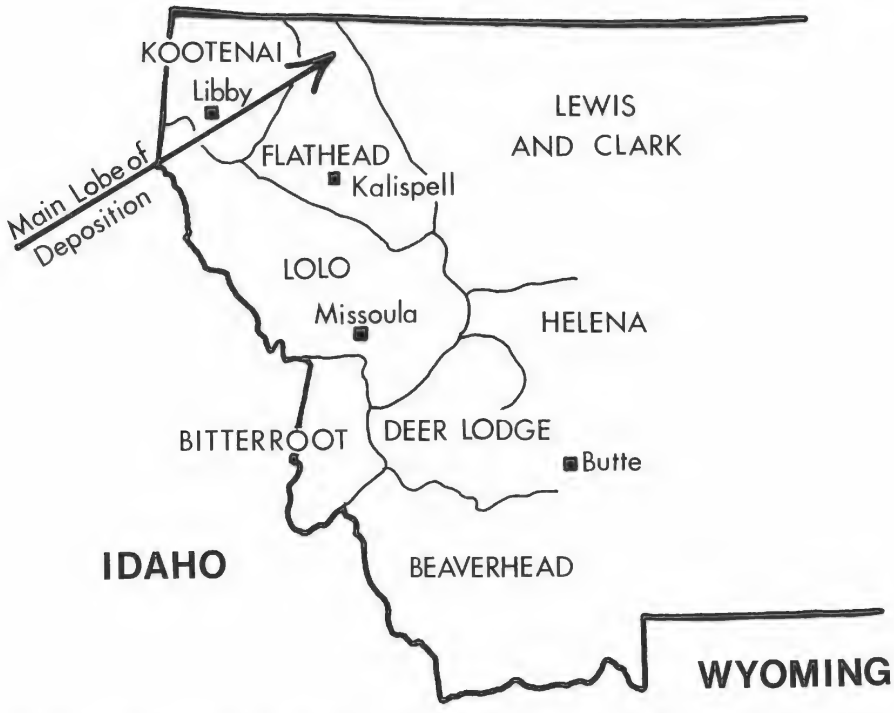


Figure 1. Location of National Forests in Montana and the main lobe of ash deposition.

shifts between the observed and expected elevation distributions within each of the four distance groups, Chi-square tests of independence were conducted.

The expected distribution of habitat series (Arno 1979) was compared with the observed distribution to determine if ash soils were more frequently associated with certain habitat types than others.

Thickness

Simple correlation coefficients were computed between the dependent variable, ash thickness, and the independent variables, associated interactions, and transformations. The magnitude of these correlations indicated which independent variables exhibited the greatest individual degree of association with ash thickness. To obtain average point estimates of ash thickness, a stepwise, least-squares procedure was used to derive a reliable prediction equation (high coefficient of determination, R^2, and low standard deviation about regression as percent of response mean).

Results

Distribution

Ash was found at elevations of 800 to 2833 m and at distances up to 365 km to the southeast and 80 km to the northwest of the line representing the main lobe, although only a few plots were north of the line.

Ash is associated with a number of habitat series as shown in Table 2. It was never

TABLE 2. Habitat series found on volcanic ash.

Habitat series	Abbreviation	Number of descriptions
Pseudotsuga menziesii	PSME	50
Picea	PICEA	4
Abies grandis	ABGR	18
Thuja plicata	THPL	25
Tsuga heterophylla	TSHE	9
Abies lasiocarpa	ABLA	215
Tsuga mertensia	TSME	3
Pinus albicaulis	PIAL	2
		326

found with the *Pinus ponderosa* or *Pinus flexilis* series nor with those habitat types within *Pseudotsuga menziesii* series that are characteristic of dry sites: *Agropyron spicatum, Festuca idahoensis*, and *Festuca scabrella.* The most common series found on ash is *Abies lasiocarpa*; approximately 70 percent of the soils described were supporting this series. The most common types within the *Abies lasiocarpa* series were *Clintonia uniflora, Xerophyllum tenax, Menziesia ferruginea*, and *Vaccinium caespitosum*, in that order.

Ash occurs on all aspects but is more common on north exposures; it is found on slope gradients from 0 to 100 percent.

Tables 3 and 4 present the frequency of occurrence of ash mantles by elevation, distance from the main lobe, habitat group, and aspect classes. The *Abies lasiocarpa-Xerophyllum tenax* and *Abies lasiocarpa-Menziesia ferruginea* types do not occur on

TABLE 3. Frequency of occurrence of ash mantles by elevation, distance from the main lobe, and habitat group class.

Habitat group	Distance from main lobe (km) 0-50	50-100	100-200	200+	Total
	Elevation class 800-1200 (m)				
PSME	14	4	0	0	18
PICEA, etc.[1]	18	7	2	0	27
ABLA	17	4	1	0	22
	49	15	3	0	67
	Elevation class 1200-1500 (m)				
PSME	4	7	7	2	20
PICEA, etc.	11	9	1	0	21
ABLA	22	18	18	0	58
	37	34	26	2	99
	Elevation class 1500-1800 (m)				
PSME	1	0	3	4	8
PICEA, etc.	1	5	0	0	6
ABLA	8	17	28	11	64
	10	22	31	15	78
	Elevation class 1800-3000 (m)				
PSME	0	1	0	3	4
PICEA, etc.	0	0	0	1	1
ABLA	5	6	16	45	72
	5	7	16	49	77
	101	78	76	66	321

[1]PICEA, ABGR, THPL, and TSRE series (5 plots of TSME and PIAL excluded).

TABLE 4. Frequency of occurrence of ash mantles by elevation, distance from main lobe, and aspect class.

Aspect	Distance from main lobe (km) 0-50	50-100	100-200	200+	Total
	Elevation class 800-1200 (m)				
North	23	4	2	0	29
East	10	5	0	0	15
South	10	3	0	0	13
West	6	3	1	0	10
	49	15	3	0	67
	Elevation class 1200-1500 (m)				
North	13	6	13	2	34
East	9	7	4	0	20
South	7	9	9	0	25
West	8	12	0	0	20
	37	34	26	2	99
	Elevation class 1500-1800 (m)				
North	0	9	10	8	27
East	2	7	11	2	22
South	5	4	6	2	17
West	3	3	4	3	13
	10	23	31	15	79
	Elevation class 1800-3000 (m)				
North	1	1	8	18	28
East	1	1	8	18	28
South	2	3	2	7	14
West	3	3	1	18	25
	7	8	17	49	81
	103	80	77	66	326

ash at low elevations anywhere in the study area. Apparently temperature, not moisture, is the major factor influencing the distribution of these habitat types.

The *Pseudotsuga menziesii* series occurs throughout western Montana (Arno 1979); however, it was found *on ash* primarily near the main lobe, seldom at either high elevations or near the southeast limit of ash distribution. A number of series (*Abies grandis, Picea* spp., *Thuja plicata*, and *Tsuga heterophylla*) were associated with ash almost exclusively near the main lobe, ostensibly because these species only occur in the very western part of the state (Arno 1979).

Ash occurs at all elevations near the main lobe, but its elevational distribution in other areas is more restricted. The observed and expected elevational distribution of ash proflies by four distance-from-the-main-lobe classes and the associated Chi-square statistics are presented in Table 5. Because of the pronounced differences between the two distributions within each distance class, all four Chi-square tests were significant at $\alpha = 0.5$. Even though elevation naturally increases with greater distance from the main lobe (expected frequency), ash profiles (observed frequency) occurred with greater frequency at increasingly higher elevations with greater distance from the main lobe, implying that the presence of ash is dependent on the interaction between elevation and distance from the main lobe.

The difference in ash occurrence between north and south slopes is more striking at great distances from the main lobe. For example, in the distance class farthest from the main lobe (> 200 km), there were 28 ash soils described on north aspects and only nine on south aspects.

TABLE 5. The observed and expected elevational distribution of ash profiles by four distance classes and associated Chi-square statistics.

	Distance from main lobe (km)							
	0-50		50-100		100-200		200+	
Elevation (m)	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
800-1200	49	34	19	43	4	27	0	3
1200-1500	36	44	44	30	34	18	3	15
1500-1800	10	15	28	20	41	23	23	35
1800-3000	5	7	9	7	21	32	74	47
	100	100	100	100	100	100	100	100
X^2_c	10.31**		23.70**		51.68**		32.22**	

**Significance at $p > .05$ since $X^2 3, .95 = 7.81$.

TABLE 6. Means and standard deviations of three independent variables by distance-from-main-lobe group.

		Distance-from-main-lobe group (km)					
Variables		0-15	20-50	55-35	90-160	165-215	220-365
Elevation (m)	Mean	1275	1240	1450	1464	1672	2154
	Standard Deviation	283	271	261	248	301	315
Slope Gradient (%)	Mean	23	34	41	33	30	27
	Standard Deviation	22	22	18	18	17	15
Ash Thickness (cm)	Mean	25	30	34	27	22	22
	Standard Deviation	11	13	14	9	7	8

Near the main lobe, ash occurs on all slope gradients, but farther from the main lobe it is not found on steep slopes. Only eight ash soils were described on steep slopes ($>$ 40 percent gradient) at 200 plus km.

The relationship between ash distribution and elevation and slope gradient is illustrated in another way. Mean and standard deviations for elevation and slope gradient over six classes of distances from the main lobe are presented in Table 6. Mean elevation increases with increasing distance from the main lobe after 20 km. Slope gradient increases to 55-85 km and decreases thereafter.

Thickness

Table 6 also lists the mean and standard deviation of ash thickness. The mean thickness increased from 22 to 34 cm, with a standard deviation from 7 to 14 cm.

Mean ash thickness increases to the 55-85 distance and decreases thereafter, indicating that the main line of deposition was probably between 55 and 85 km south of where the line was actually drawn. This is also the area where thick ash deposits have been reported and where precipitation is greatest in Montana (the vicinity of Trout Creek).

Simple correlation coefficients between the "best" six independent variables and ash thickness are presented in Table 7. The correlations of interest are found in the last column, where it can be seen that x_4 (slope x (moisture index $-5)^2$) and x_1 (slope) are most highly correlated with ash thickness. As discussed in the methods section, habitat types were ordinated by two indexes, moisture and temperature, each on a scale from 0 to 10.

TABLE 7. Simple correlation coefficients between selected independent variables and ash thickness (y).

	X_1	X_2	X_3	X_4	X_5	X_6	Y
X_1	1.0	.09	-.04	.58	.93	-.11	.35
X_2		1.0	-.35	.73	.05	.02	.27
X_3			1.0	-.26	.06	.06	-.24
X_4				1.0	.50	-.03	.39
X_5					1.0	-.09	.26
X_6						1.0	-.14
Y							1.0

Where: X_1 = slope; X_2 = (moisture index - 5)^2
X_3 = distance from lobe; $X_4 = X_1 * X_2$
$X_5 = X_1 *$ temperature index; $X_6 = 180° -$ aspect

After entering all six independent variables, only 22 percent of the total variation in ash thickness was accounted for.

Because average point estimates of ash thickness could not be predicted with high reliability a discriminant analysis was performed to classify data points into six ash-thickness ranges: 8-19, 20-29, 30-39, 40-49, 50-59, and 60-69 cm. Two discriminant functions were produced, which explains 91 percent of the total variation in ash thickness and consists of a linear combination of the original six independent variables. The two functions are able to classify data points correctly into the six ash-thickness ranges 38 percent of the time, with adequate prediction in the two end ranges only (8-19 cm and 60-69 cm ranges, respectively). Therefore, ash-thickness ranges could not be estimated reliably by the independent variables used in this study.

Discussion

Figure 2 illustrates the distribution of ash mantles in western Montana. Near Libby, which is in line with the main lobe of deposition, ash occurs at all elevations, slope gradients and aspects, and in association with *Pseudotsuga menziesii, Abies grandis, Picea, Tsuga heterophylla, Thuja plicata,* and *Abies lasiocarpa* habitat series. In the southern and southeastern limits of the ash's range (Butte, 350 km to the southeast of Libby), the ash is found only on high elevation sites (greater than 2000 m) which are on north aspects, have gentle gradients, and are in association with the *Abies lasiocarpa* habitat series.

Although precipitation was not measured as part of this study, it is evident that the ash and precipitation distribution patterns are related; areas of widespread ash, the mountains in the northwest corner of the state, are also areas of greatest precipitation (Ross and Hunter 1976).

The role precipitation played in ash distribution is probably two-fold. Rain and snow filtered ash out of the atmosphere, and areas of higher precipitation were generally those of more lush vegetation where ash was protected from erosion.

We have not attempted to stratify the data by the underlying material, although we recognize that in some areas there is a relationship between ash distribution and limestone. In the Garnet Mountains, for example, ash occurs over limestone at elevations greater than 2100 m, although it occurs over non-calcareous materials at elevations greater than about 1800 m. The influence limestone has on the weathering of ash and the relationship between ash and underlying materials needs further study.

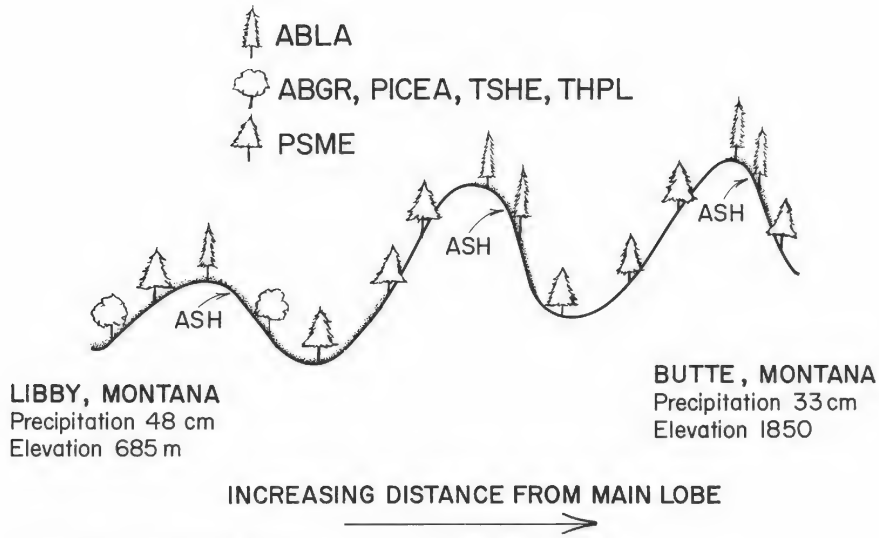


Figure 2. Ash distribution in the mountains of western Montana.

The thickness of the ash could not be accurately predicted from the variables we measured: elevation, geographic location relative to the main area of deposition, habitat type, aspect and slope gradient. There are a number of possible reasons for this. Only 7 of the 326 profiles studied had ash mantles 10 cm or less thick, and none were less than eight. Thus, one part of the possible range of thickness is missing.

Another possible reason for poor prediction equations was in our method of calculating the distance from the main line of deposition. We used the main lobe of the Mazama ash-fall to establish the line from which we located the plots. Although Mazama ash is the dominant ash in western Montana (Nimlos 1980), it is not the only one.

The zone of maximum thickness in Montana is probably in the vicinity of Trout Creek, Montana. But it is not known whether this is because the main line of wind currents carrying ash ran through this area or because this is the area of highest precipitation on the western boundary of the state, or both.

Another unknown is the purity of the ash deposits. In the area in line with the main lobe of deposition, the soil properties associated with ash soils, low density, low coarse fragment content, abrupt boundary, etc., are better expressed than in the southern limit of ash distribution. The dilution of ash, probably, is by other loessial material and mixing with lower horizons.

Acknowledgments

We thank soil scientists of the Forest Service and the Soil Conservation Service for providing their soil descriptions.

Literature Cited

Arno, S. E. 1979. Forest regions of Montana. USDA, Forest Service, Research paper, INT-218.
Nimlos, T. J. 1980. Volcanic ash soils. Western Wildlands 6(3):22-24. Publ. by Montana For. and Cons. Exp. Sta., Missoula, Mt.

———. 1981. Volcanic ash soils in Montana. Bull. 45 Mont. For. and Conser. Exp. Sta., Univ. of Montana, Missoula, Mt.
Ottersberg, R. J. 1977. Amorphous character in twenty western Montana forest soils with apparent eolian influence. Mont. St. Univ., Bozeman, M.S. thesis.
Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. USDA, Forest Service Gen. Tech. Rept. INT-134.
Ross, R. L., and H. E. Hunter. 1976. Climax vegetation of Montana. USDA, SCS, Bozeman, Mt.

Received April 10, 1981
Accepted for publication July 17, 1981

Roger A. Woodruff[1]
and
Barry L. Keller
Department of Biology
Idaho State University
Pocatello, Idaho 83209

Dispersal, Daily Activity, and Home Range of Coyotes in Southeastern Idaho

Abstract
Data on dispersal, home range, and daily activity patterns were collected during 11 months for 15 coyotes (*Canis latrans*) radio-collared on the Idaho National Engineering Laboratory Site. Dispersal distances ranged from 0 to 57 km for 10 juveniles. Mean home range with standard error for four adult females was 45.9 $\pm$ 1.7 km^2 by the ellipse method and 29.3 $\pm$ 2.4 km^2 by the modified minimum area method. Home range of one adult male was 133.0 km^2 and 80.6 km^2 by the two methods, respectively. When more than 100 relocations were available, the modified minimum area method appeared to estimate home range size more accurately. During the summer, coyotes were most active near dawn and dusk. A general lack of activity was noted from 1100 h to 1500 h MST. Analysis of 15 minute interval fixes obtained over a 24-hour period suggested that some areas within the home range received more intensive use than others, particularly areas around resting points.

Introduction

The coyote is one of the most controversial predators in North America and has a dramatic economic effect upon the livestock industry. Since the Presidential ban of toxicants in 1972, Federal control efforts have shifted emphasis from general population reduction to selectively addressing problem areas and removing depredating individuals. Selective control requires a thorough knowledge of coyote behavior and movements.

This study, the third in a series of coyote home range investigations on the Idaho National Engineering Laboratory (INEL) Site, was designed to study coyote movements in southeastern Idaho. Edwards (1975) and Rucker (1975), in two successive telemetry studies on the Site, estimated coyote home range size and shape. In this study, we increased the number of radio-collared animals and the number and intensity of fixes obtained on individual coyotes. In addition to data on dispersal and daily activity patterns, we gathered information on 24-hour activity studies and compared these data with home range information obtained over a longer duration to judge whether several 24-hour studies might be sufficient to delineate home range. Such short term analyses could be used to ascertain whether specific vegetational or topographic features were selected by coyotes. Other investigators in our group have now attempted to relate the time a coyote spends in an area to the biological requirements of this canid (Laundré and Keller 1981, Wilkosz and Anderson 1979, Wilkosz 1980).

Study Area

The Idaho National Engineering Laboratory Site is located on the Upper Snake River

[1]Present address: U.S. Sheep Experiment Station, Dubois, Idaho 83423.

Plain, 56 km west of Idaho Falls in southeastern Idaho. The site encompasses an area of approximately 2315 km^2 and is characterized by rolling to broken plains interspersed with volcanic craters and cones. Vegetation is classified as northern cool-desert type with big sagebrush (*Artemisia tridentata*)-grass communities the dominant association (McBride *et al.* 1978). Annual precipitation averages 21 cm with the maximum occurring in May and June and the minimum in July and August.

Trapping

Studies of coyote population parameters (R. Davison, pers. comm.) and the telemetry data reported here were conducted independently on animals trapped by a U.S. Fish and Wildlife Service trapper. Three traplines, incorporating a total of 200 Victor number 3 steel traps each equipped with a tranquilizer tab (Balser 1965), were used to capture coyotes. Traps were checked every morning for 23 days during October 1975. Coyotes were removed from the traps and placed in wire cages for processing at Atomic City, Idaho, where we estimated age (Gier 1968) and noted sex, weight, and general condition. Each coyote was eartagged, fitted with a 164 MHz transmitter collar equipped with a mortality switch (Kotz *et al.* 1973), and released the following morning at the point of capture.

Tracking

Semi-permanent telemetry stations were constructed at five locations on or near the INEL Site. Each station was placed on a prominent hill or butte and consisted of a weatherproof shelter, a 9.2 m mast topped with two matched yagi antennae, and a hybrid junction to facilitate determination of signal direction. Reception range from the stations varied from 8-22 km. A mobile unit equipped with a five element yagi antenna on a 2 m mast was used for close range locations. An AVM model LA-12 receiver was used in the vehicle and stations.

We observed activity patterns during the summer of 1976, from 1 July until 20 August. Triangulation points were obtained by one observer who took the first azimuth from a position along a secondary road and then moved 0.3-0.8 km to obtain the second bearing. Elapsed time between compass readings varied from 1-5 minutes. Two observers alternated six-hour shifts to obtain triangulations every 15 minutes during a 24-hour observation period. The mobile unit was used extensively in these studies to maintain minimum reception distance.

Mapping

Telemetry fixes, capture and recovery sites, and visual sightings were plotted on topographic maps for home range analysis. The ellipse method (Gipson and Sealander 1972) and the modified minimum area method (Harvey and Barbour 1965) were used to calculate home range size.

Location points obtained on a daily basis and those obtained from the 24-hour activity studies were added in various combinations to allow comparison between the ellipse and modified minimum area methods for estimating home range size. First, all daily locations for each coyote were used to calculate home range sizes by both methods. Relocations obtained from the first 24-hour study periods were added to these points, and home ranges were again calculated. This process was repeated until all relocations had been plotted. In addition, home range estimations were made with

points obtained from the activity studies. Significant differences noted in the text are at $P < 0.05$.

Results

Trapping

Twelve male and 12 female coyotes were captured during approximately 3700 trap nights. Radio collars were placed on 23 animals. Age classes ranged from juvenile to old adult (10-12 yrs.), with juveniles comprising 42 percent of the animals.

Home Range and Movements

Sufficient data were gathered to calculate the home ranges of seven coyotes (Table 1). The ellipse and modified minimum area methods gave significantly different estimates (paired t test, $P < 0.05$) of home range size, with the ellipse yielding a higher value even when activity data were included in the analysis. Figure 1 graphically compares home range estimates for coyote 26, as obtained by the two methods. Minimums of 150-175 locations were needed in this case to accurately estimate home range size, as evidenced by the zone where home range ceases to increase significantly. Several home range estimates for a single animal, based on differing numbers of points, were obtained by both methods. Points obtained from the 24-hour tracking periods plotted as individual units yielded estimates smaller than those obtained from a comparable number of points which included locations obtained on a one per day basis.

Mean home range size for four adult females with standard error was 29.3 ± 2.4 km^2, and 45.8 ± 1.7 km^2 for the modified minimum area and ellipse methods, respectively; therefore, the ellipse method results in a 56 percent size increase.

Capture points were analyzed with respect to their location in the home range. The modified minimum area method was used to estimate home range boundaries during the analysis. In 50 percent of the cases, the capture point was either outside or on the border of the home range. In the remaining cases, the capture point was not more than 0.5 km inside the border.

TABLE 1. Sex, number of months tracked, and home range estimates obtained by the ellipse and modified minimum area methods for seven radio-collared coyotes on the INEL Site, Idaho. Variation in estimates obtained for three animals by each method occurs from combining activity studies with single point location data.

Coyote	Sex	Months tracked	Points used[1]	Number of relocations	Home range size (km^2) Ellipse method	Modified minimum area method
24	M	10	T	41	8.5	5.3
25	F	8	T	39	50.0	31.3
34	F	7	T	37	41.5	22.1
37	F	10	T	39	45.8	32.0
22	F	11	D	19	40.6	23.5
22			D,A	60	42.7	28.8
22			T	105	46.3	31.7
22			A,B	86	32.9	22.1
26	F	12	D	64	26.8	17.7
26			T	226	37.0	27.6
26			T,A	162	32.8	26.2
38	M	14	D	15	62.0	14.2
38			T	135	133.0	80.6
38			T,A	120	59.5	52.0

[1]T = all points; TA = total, all activity; A = activity study 1; B = activity study 2; D = daily fixes.

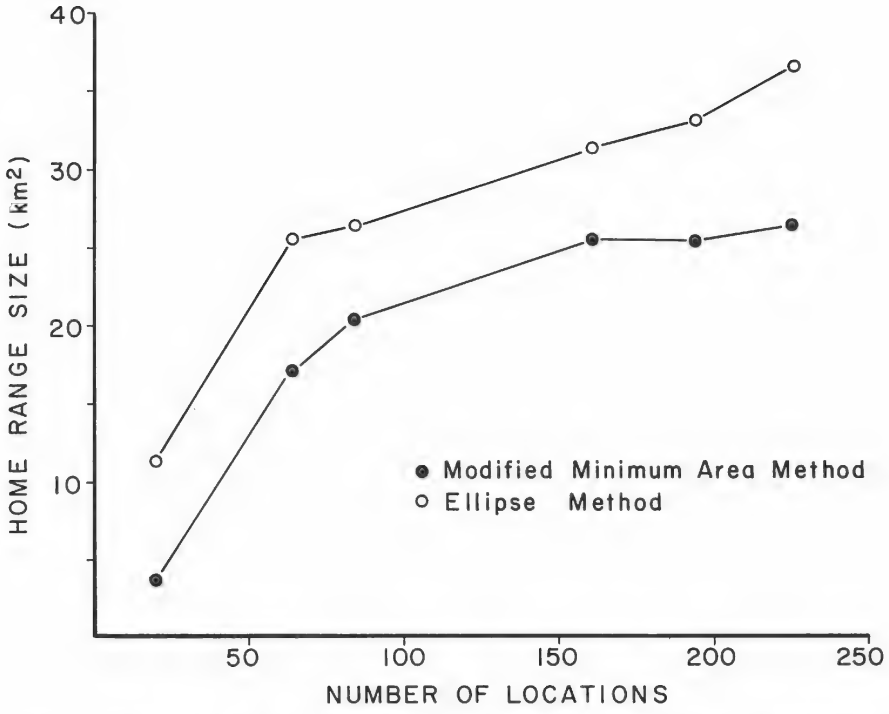


Figure 1. Home range size calculated by two methods in relation to the number of relocations for coyote 26 on the INEL Site, Idaho.

Straight-line dispersal distances of juveniles were calculated and are compared in Table 2. Although a difference of nearly 30 km exists between mean dispersal distances for males and females tracked for at least 4 months, a t test revealed no significant difference ($t = 2.750$, $df = 4$).

Seven of 10 juveniles displayed dispersal tendencies, and in all but one case, dispersal was in an outward direction from the boundaries of the Site. Coyotes 32 and

TABLE 2. Sex, months tracked, and straight-line dispersal for six radio-collared juvenile coyotes on the INEL Site, Idaho.

Coyote	Sex	Months tracked	Straight-line dispersal distance (km)
26	F	12	0.0
30	F	4	18.1
44	F	5	25.2
24	M	14	32.9
35	M	12	39.2
40	M	8	32.9 (57.0)[a]

Mean dispersal distance for males = 43.0
Mean dispersal distance for females = 14.4

[a]Known point of farthest movement.

29 were killed within four weeks of their release; no directional information was inferred from either. Coyote 26 was tracked for more than one year, and her location at death was calculated to be within the home range boundaries. All males exhibited dispersal of more than 30 km. Coyote 40 moved as far as 57 km from his capture point but was killed along a highway at a distance of 32.9 km from point of capture. Coyote 24 moved 33 km southeast along the INEL Site boundary, where he established a home range and remained until killed in December 1976. Coyote 35 repeatedly moved between his approximate capture point and a point 11 km south of the Site, and was eventually killed 39.2 km from his capture point. No dispersing radio-collared coyotes survived to the end of this study.

Daily Activity

Table 3 summarizes mean, maximum, and minimum straight-line distance movements of four coyotes obtained at 15-minute intervals during the 24-hour tracking periods. Mean distance moved in 15 minutes with standard error was 0.73 ± 0.04 km and 0.86 ± 0.09 km for females and males, respectively. No significant difference was found between these values. Combined, they give 0.77 ± 0.04 km as the mean straight-line distance traveled during a 15-minute interval. Table 3 presents a compilation of 15-minute interval movements totaled for each 24-hour tracking period, thus yielding a minimum daily distance traveled by each animal. No significant difference was found between mean daily summertime distances moved by males or females. Combined data indicate that the mean minimum daily distance with standard error is 27.6 ± 2.7 km.

TABLE 3. Sex, maximum, minimum, mean (± SE), and total straight-line distances (km) moved while active during 15-minute intervals by four radio-collared coyotes on the ISEL Site, Idaho. The sample size indicates the number of fixes or 15-minute observations used to calculate the mean. Numbers enclosed in parentheses indicate the number of 24-hour monitoring periods.

		Straight-line distance moved during a 15-minute interval (km)				15-minute interval distance totaled for a 24-hour period (km)	
Coyote	Sex	Max.	Min.	Sample size	Mean ± S.E.		
22	F	2.60	0.10	49	0.74 ± 0.09	26.01 (1)	27.31 (2)
26	F	2.79	0.01	111	0.72 ± 0.05	33.73 (1)	19.85 (2)
24	M	1.85	0.23	12	0.75 ± 0.17	17.60 (1)	———
38	M	3.75	0.08	54	0.89 ± 0.10	33.11 (1)	35.83 (2)

Distance moved during 30-minute intervals was plotted against time of day to determine daily activity patterns of coyotes. Times that animals were active varied among individuals and among different activity studies for the same individual. Figure 2 is a composite activity graph which combines data obtained from all animals. The general trends shown by this figure are: 1) a major peak of activity at and immediately following sunset; 2) a definite decline in activity during midday, particularly from 1100 h to 1500 h MST; 3) a minor peak of activity near sunrise with a fairly high amount of activity during the pre-sunrise hours.

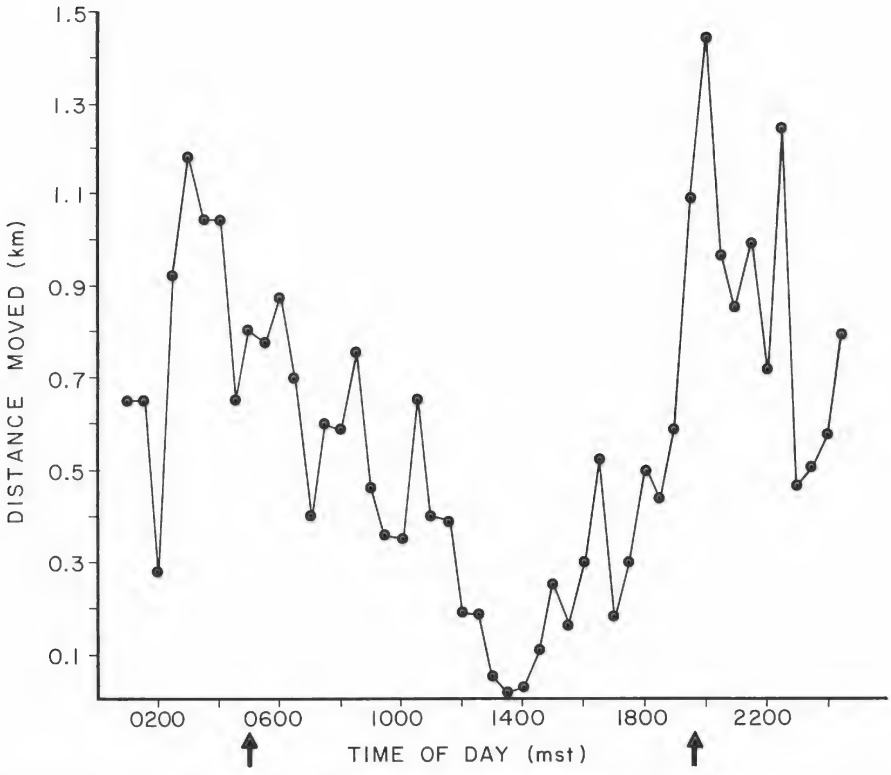


Figure 2. Mean straight-line ½-hour movements (km) in relation to time of day for four radio-collared coyotes (22, 24, 26, and 38). The figure is a composite of the results of 10 monitoring periods during summer, 1976. Arrows indicate average sunrise and sunset times.

Discussion

Maximum dispersal from the capture point for juveniles in this study was 57.0 km. This distance is much less than that reported by Hibler and Knowlton (1974) for coyotes in Utah, where two animals dispersed 217 and 290 km. In California, Hawthorne (1971) reported average dispersal of juvenile male and female coyotes as 5.2 and 6.4 km, respectively. The longest movement, 140 km, was recorded for a juvenile male, but no other coyote dispersed more than 24 km. In Wyoming and Montana, Robinson and Grand (1958) noted that movements of 80-160 km were not uncommon, and Chesness and Bremicker (1974) found dispersal in Minnesota to range up to 58 km. These figures indicate a large variability in coyote dispersal and the capability of juveniles to disperse long distances from natal areas. Whether this variability reflects geographic differences in niche requirements, genetic differences in dispersers, or is an artifact of methodology needs to be investigated.

Capture points of juveniles were clustered in two general locations on the Site, and dispersal out of both areas was in the direction of the nearest Site boundary. Knowlton (1972) observed coyotes moving from areas of higher population density into areas of lower density. Hunting and removal of coyotes in the areas adjacent to the INEL

Site may have resulted in the same phenomenon in our study, particularly during late autumn and winter, when dispersed juveniles and removal of coyotes on adjacent lands are greatest.

Daily activity of four animals was monitored during July and August 1976, and additional data have been made available by Laundré (1979), who continued this study. During summer, coyotes may be active any time of the day or night, although activity was more common near dusk and dawn. Two animals exhibited increased nighttime activity. Gipson and Sealander (1972) observed peaks of activity at approximately the same times, but the general lack of activity at midday observed during this study was not as apparent in the Arkansas data. Winter activity patterns may differ from those reported herein as a result of snow depth, photoperiod, or changes in prey behavior, as Laundré and Keller (1981) report seasonal variability in daily activity patterns.

After the Presidential ban of toxicants on Federal lands, methods of predator control became directed more toward removing individual offenders than toward general population control. A quantitative knowledge of coyote range and daily movements can help depredation control agencies determine where to remove problem animals most effectively. In this study, radio-collared coyotes traveled an average of 28 km daily. This value is considered to be a minimum distance, as it was obtained by summing straight-line movements of 15-minute intervals. The actual distances traveled are undoubtedly greater. The greatest distance moved in 24 hours was 35.8 km. On two other occasions a coyote was observed to move more than 30 km in a day.

Analysis of capture points revealed that no coyote was captured in a heavily used or preferred area of the home range. This observation is similar to that documented by Hibler and Knowlton (1974) and Rucker (1975). A combination of familiarity with the heavily used parts of the home range and increased awareness of scent stations outside these areas may contribute to a higher trapability of animals in fringe areas.

Home range was estimated for two juveniles followed intensively during this study. Female coyote 26 established a home range on the Site, and her capture point was within the home range boundaries. Most of the locations for this animal were obtained after she became one year old; her home range did not differ significantly in size from those of adult females. Male coyote 24 dispersed about 33 km off the Site and established a home range adjacent to cultivated land. The home range of this animal was estimated as approximately 10 and 20 percent of the home range sizes for the adult male (38) and juvenile female (26), respectively (Table 1). A variety of factors may have contributed to this low estimate. The non-arable habitat that coyote 24 utilized was surrounded by farmland and encompassed an area of only 15 km^2. Concentrations of lagomorphs appeared visually greater there than in desert areas of comparable size. This may have reduced the length of daily excursions in search of food, thus affecting the size of the home range. Human activities in the area may also have influenced his movements as compared to coyotes living in uninhabited areas.

Gipson and Sealander (1972) found coyote home range in Arkansas, as determined by the ellipse method, to be 20 to 35 percent of comparable estimates obtained in our study. Chesness and Bremicker (1974), using the minimum area method (Mohr 1947), found that home ranges of adult female and male coyotes in Minnesota averaged 16.1

km^2 and 67.1 km^2, respectively. However, the minimum area method yields estimates twice as large as the modified minimum area method (Harvey and Barbour 1965, Rucker 1975). If the Minnesota figures are adjusted accordingly, coyote home ranges in Idaho averaged 2.5 to 3.5 times larger. Estimates obtained in our study substantiate those of Rucker (1975) and Edwards (1975) in earlier telemetry studies on the INEL Site. It appears that the size of the area used by a coyote may be a function of population density, food base, differences in habitat, pressure by man, or a combination of these factors.

In this study, a total of 150-175 locations was needed to describe coyote home range accurately. However, time span of the sampling period is also an important factor to consider as it is unlikely that a coyote would utilize his entire home range during one or two 24-hour periods. For example, when daily locations which had been obtained over a period of nine months were combined with locations obtained during the first 24-hour activity study for coyote 22, a total of 60 points and an area of 42.7 km^2 were observed. When locations from the first and second activity studies were combined, a total of 86 points and an area of 33.0 km^2 were observed. Although 26 more location points were obtained in the latter, the calculated home range was smaller. Omission of data during a short sample period illustrates the importance of maximizing and intensifying the collection period to accurately identify coyote home range This would be particularly true of a highly dynamic or shifting home range.

Comparisons of the modified minimum area and ellipse methods show that the ellipse method consistently yielded larger estimates of home range size, even when over 200 relocations were used in the calculations. Our results agree with those of Jennrich and Turner (1969), lending support to the contention that telemetry methodology needs to be standardized. Rucker (1975) contends that of the two methods, the modified minimum method is superior in describing both shape and location of the home range. The ellipse method tends to include areas where no relocations are made and excludes others where relocations were present; our data suggest that home range size begins to increase at a much reduced rate in the region of 150-175 location points for both methods. Assuming that the modified minimum area method estimated home range accurately, we conclude that the ellipse method would have yielded an accurate estimate at approximately 50 points. These calculations substantiate Jennrich and Turners' (1969) conclusion that estimations based on polygon methods will tend to underestimate home range size when only a small number of locations are used. Therefore, when working with few data, especially those collected over several 24-hour studies, the ellipse method may provide a more accurate estimation of home range size. The modified minimum area method may be a superior indicator of home range size and shape when larger numbers of points (100 or more) are available.

Future studies should attempt to describe coyote movements via activity studies. Current methods of home range calculation tend to ignore specific habitat utilization, even though biotelemetry allows monitoring of virtually all activity. More information could be realized by employing the methodology of Fossey (1974) and Laundré and Keller (1981), who mapped home range of animals relative to habitat usage. Wildlife managers still lack a definitive assessment of coyote movement in relation to the niche requirements of the individual animals.

Acknowledgments

We thank F. Knowlton, U.S. Fish and Wildlife Service; R. Davison, Utah State University; J. Laundré, Idaho State University; and O. D. Markham, Idaho National Engineering Laboratory, Radiological and Environmental Sciences Laboratory, for their help and cooperation throughout the study. This research was funded by an Office of Health and Environmental Research, U.S. Department of Energy, grant to Keller, and is a contribution of the Idaho National Engineering Laboratory Site Ecological Program. Part of the travel was made possible by a grant funded through Kirkland and Ellis, Chicago, Illinois, to purchase a vehicle.

Literature Cited

Balser, D. S. 1965. Tranquilizer tabs for capturing wild carnivores. J. Wildl. Manage. 29: 438-442.

Chesness, R. A., and T. P. Bremicker. 1974. Home Range Territoriality and Sociability of Coyotes in North-central Minnesota. Paper presented at Coyote Workshop, Denver, Colo., Minn. Dept. Nat. Resources, Grand Rapids, MN.

Edwards, L. L. 1975. Home Range of the Coyote in Southern Idaho. Idaho State Univ., M.S. thesis.

Fossey, D. 1974. Observations on the home range of one group of mountain gorillas. Anim. Behav. 22: 568-581.

Gier, H. T. 1968. Coyotes in Kansas. Revised. Kansas State Coll. Agr. Expt. Sta. Bull. 393.

Gipson, P. S., and J. A. Sealander. 1972. Home range and activity of the Coyote (*Canis latrans frustror*) in Arkansas, pp. 82-95 *in*: Proceedings of the 26th Annual Conference of S.E. Association of Game and Fish Commissioners.

Harvey, M. J., and R. W. Barbour. 1965. Home range of *Microtus ochrogaster* as determined by a modified minimum area method. J. Mammal. 46: 398-402.

Hawthorne, V. M. 1971. Coyote movements in Sagehen Creek Basin, northeastern California. Calif. Fish and Game 57: 154-161.

Hibler, S. J., and F. F. Knowlton. 1974. Preliminary Interpretation of Coyote Movement Patterns. Paper presented at Coyote Workshop, Denver, Colo., Dept. Wildl. Sci., Utah State Univ., Logan, Utah.

Jennrich, R. I., and R. B. Turner. 1969. Measurement of non-circular home range. J. Theoret. Biol. 22: 227-237.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. J. Wildl. Manage. 36: 369-382.

Kolz, A. L., G. W. Corner, and R. E. Johnson. 1973. A Multiple-use Wildlife Transmitter. Spec. Sci. Dept. Wildl. No. 163 Denver Wildlife Res. Ctr.

Laundré, J. W. 1979. A Behavioral Study of Home Range Utilization by Coyotes on the INEL Site in Southeastern Idaho. Idaho State Univ., Ph.D. thesis.

———, and B. L. Keller. 1981. Home-range use by coyotes in Idaho. Anim. Behav. 29: 449-461.

McBride, R., N. R. French, A. H. Dahl, and J. E. Detmer. 1978. Vegetation Types and Surface Soils of the Idaho National Engineering Laboratory Site. IDO-12085, National Technical Information Service, Springfield, Va.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Nat. 37: 223-249.

Robinson, W. B., and E. F. Grand. 1958. Comparative movements of bobcats and coyotes as disclosed by tagging. J. Wildl. Manage. 22: 117-122.

Rucker, R. L. 1975. The Home Range of the Coyote (*Canis latrans*) and its Method of Calculation. Idaho State Univ., M.S. thesis.

Wilkosz, R. J. 1980. Coyote Habitat Preferences on the Idaho National Engineering Laboratory Site in Southeastern Idaho. Idaho State Univ., M.S. thesis.

———, and J. E. Anderson. 1979. Coyote habitat preferences on the Idaho National Engineering Laboratory Site. Pp. 59-60 *in:* O. D. Markham and W. J. Arthur (eds). Proceedings of the Symposium on Idaho National Engineering Laboratory Ecology Programs. IDO-12088, National Technical Information Service, Springfield, Va.

Received July 21, 1980
Accepted for publication October 28, 1980

Thomas A. Hanley[1]
College of Forest Resources
University of Washington
Seattle, Washington 98105

Cervid Activity Patterns in Relation to Foraging Constraints: Western Washington

Abstract

Foraging group size and temporal/spatial patterns of activity by reproductive female Rocky Mountain elk (*Cervus elaphus nelsoni*) and black-tailed deer (*Odocoileus hemionus columbianus*) were related to seasonal changes in forage availability and quality during May through October. Seasonal patterns of daily activity regimes indicated that food selection, consumption, and processing were the major factors constraining elk and deer habitat use. Both elk and deer reacted similarly to these constraints. Seasonal activity patterns and foraging group sizes indicated that searching effort increased as forage quality decreased, and that in September-October foraging emphasis shifted from individual plants to microhabitats where plant phenology was delayed relative to average conditions.

Knowledge of the relative importance of various ecologic constraints within which animals operate is important for understanding animal-habitat relationships. Foraging constraints are one set of factors which determine an animal's patterns of activity and habitat use. Although all animals must secure food, there remains on a case by case basis some question as to the degree that feeding dominates the daily activity budget. In those cases in which feeding does dominate the daily activity budget (i.e., Schoener's (1971) "energy maximizer"), the distribution of food quantity and quality in time and space is likely to be most useful in understanding the animal's activity and habitat use patterns.

There is reason to believe that foraging constraints should dominate the behavior patterns of reproductive female ruminants in temperate environments during spring through fall. Since voluntary food intake is limited by food passage rate, which is a function of diet quality (Van Soest 1965), ruminants in temperate climates face a difficult situation during winter. They cannot compensate for poor quality forage by eating a greater quantity; rather, they must eat less. Deer usually take in less energy than they expend during winter and consequently lose weight (Mitchell *et al.* 1976, Wallmo *et al.* 1977, Short 1981). Therefore, body reserves (e.g., fat and muscle tissue) accumulated prior to winter are an important aspect of a deer's seasonal nutritional strategy. Although barren females and adult males may replenish their body reserves throughout spring, summer, and fall (Mitchell *et al.* 1976), reproductive females bear high gestation and lactation costs during spring and summer, respectively (Moen 1973). Thus, reproductive females face relatively high nutritive demands throughout the year (Mitchell *et al.* 1976), and foraging constraints must account for a large proportion of their daily activity budgets when forage is of sufficient quality that weight gains are possible. Evidence of this hypothesis would be of value to both ungulate and feeding ecologists and land managers by improving the understanding of deer-habitat re-

[1]Present address: USDA, Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, P.O. Box 909, Juneau, Alaska 99802.

lationships on spring, summer, and fall ranges.

This report provides some empirical support of the hypothesis that foraging constraints dominate the daily activity of female deer during spring through fall. It is based on data collected incidental to a larger investigation of food and habitat selection by Rocky Mountain elk and black-tailed deer in western Washington (Hanley 1980). Data are provided herein on the relationships between seasonal changes in forage quantity and quality and corresponding changes in foraging group size and temporal/spatial patterns of foraging activity. It is important to note that forage quantity (availability of current annual growth) was lowest in May, increased rapidly to its peak in July, and steadily decreased through October. Forage quality (measured in terms of nitrogen content, cell wall constituents, and dry matter digestibility) was greatest during the period of most active plant growth (May and June) and steadily declined as time progressed. Seasonal flucuations in both forage quantity and quality were greatest for herbaceous vegetation (forbs and graminoids) and least for browse (shrubs and conifers). Elk diets were dominated by herbaceous forage, whereas deer diets were dominated by browse.

Study Area and Methods

Study Area

The study was conducted during the months of May through October within a 2000-ha area in the Cedar River Watershed on the western slope of the Cascade Range in west-central Washington. Elevation ranged from approximately 850-1250 m. Annual precipitation averaged approximately 250 cm. Daily air temperatures ranged from a July mean maximum of –5°C to a January mean minimum of –20.6°C (Franklin and Dyrness 1973). The vegetation consisted of a mosaic of seral stages of the *Abies amabilis* Zone forest (*sensu* Franklin and Dyrness 1973). The unlogged virgin forest was approximately 450-550 years old and consisted of an overstory dominated by *Tsuga heterophylla* and *Abies amabilis*, with an understory dominated by *Abies amabilis* seedlings and ericaceous shrubs, most notably *Vaccinium ovalifolium, Vaccinium membranaceum,* and *Menziesia ferruginea.* Seral stages resulting from clearcut logging were dominated by forbs and shrubs until canopy crown closure of the regenerating conifers.

The area was used as summer range (usually May through October or November, depending on snow conditions) by elk and deer which wintered in the valleys below. The area was selected for intensive study because of its relatively great diversity of seral stages and ease of access by logging roads; it was believed to be representative of elk and deer summer range on the west slope of the Cascade Range in western Washington. The Cedar River Watershed is managed by the City of Seattle. Public access and hunting are not permitted, and elk and deer are fairly accustomed to logging traffic. Therefore, study animals were relatively free from human harassment.

Data Collection

Both radio telemetry (Tester *et al.* 1964) data and visual observations provide the data for the present report. A bivariate, orthogonal coordinate system dividing the study area into a set square, 4.05-ha cells provided a means of systematically referencing the location of any observation. All observations of elk and deer were re-

corded on a standardized data form which recorded the following data: animal number (if marked), date, time, location in coordinate system, activity code, and group composition. Activity data were recorded for adult and yearling animals only and consisted of 1272 observations of elk and 783 observations of deer.

The difference in constancy of signal strength from an inactive versus an active radio-collared animal is readily apparent when a continuous chart of reception strength (measured in microamperes) is plotted by a chart recorder (Schoen 1977). Data of this nature were obtained from two adult animals, one female elk with one calf and one female deer with one fawn. The total hours of data collected for each animal were 1364 and 1122, respectively. The data were analyzed as "activity" or "inactivity" determined at systematic intervals of 15 minutes. Both animals also were located with reference to the coordinate system by repeated triangulations with a hand held "yagi" antenna three times daily: once in the early morning (approximately 0800), once at midday (approximately 1300), and once in late evening (approximately 2000). The female elk was located in this manner a total of 382 times; the female deer was located 423 times.

Data Analysis

Average group size (number of individuals in a group of animals) was determined monthly from all observed groups containing one or more adult or yearling female (male only groups were not included). Fawns or calves were not included in group totals. Lone individuals constituted a "group" of one. Data obtained from radio-located animals were not used in calculating average group sizes.

The proportional amount of time the animals allocated to certain types of activity was determined by dividing the total number of visual observations of animals engaged in that activity by the total number of observations of animals engaged in any activity. The types of activity quantified were the following: foraging (actively consuming or actively searching for food), traveling (while not foraging), and other (e.g., nursing, playing, etc.).

Temporal and spatial components of habitat use were examined on a monthly basis. Since these data were obtained from only two animals (one female elk and one female deer), rigorous statistical analyses were not warranted. Rather, their value was in the seasonal patterns they yielded. In calculating means, activity data were stratified by hourly intervals (for percentage of time spent active) or 4-hr periods (for average duration of activity bouts and inactivity bouts) daily to reduce any bias introduced by an unequal distribution of the number of observations throughout an average day. Daily distance traveled was determined by calculating the average minimum distance traveled by each animal between successive radio-locations. This distance was calculated by determining the number of 4.05-ha cells between locations and multiplying by 201.2 m, the length of one side of a square 4.05-ha cell. All minimum distances traveled between successive morning and afternoon, afternoon and evening, and evening and next morning observations were determined, and their means calculated. These provided estimates of average minimum distance traveled during the morning, afternoon, and night, respectively. The total of these three averages provided the average minimum distance traveled by each animal during a 24-hr period.

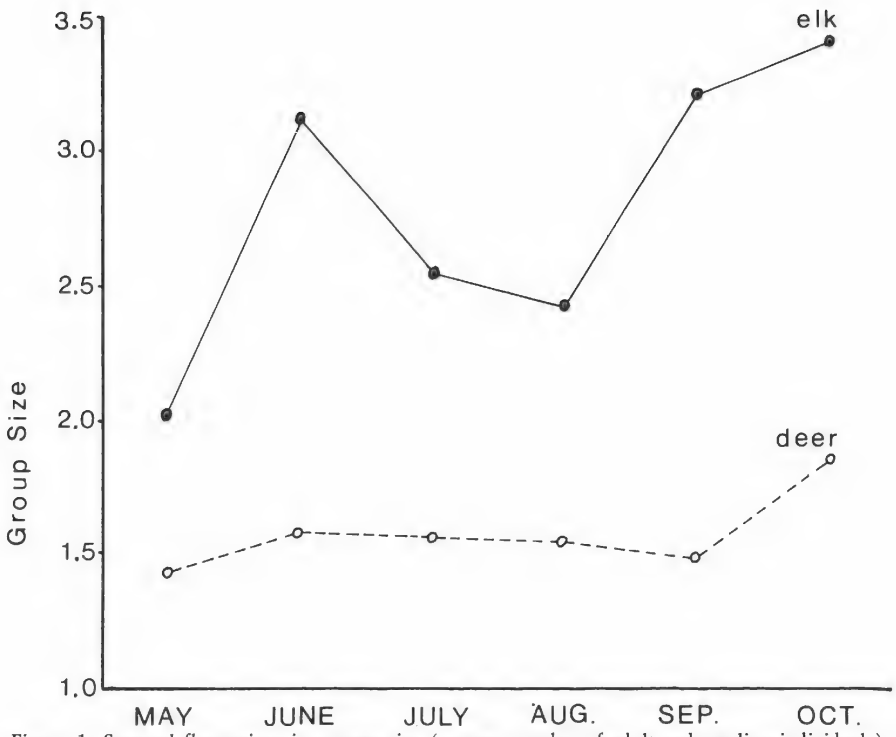


Figure 1. Seasonal fluctuations in average size (average number of adult and yearling individuals) of elk and deer groups.

Results and Discussion

A principal advantage of large group size is a greater ability to detect predators (Jarman 1974, Geist 1974, Estes 1974), which should be of greater importance to elk than to deer (because the larger body size of elk makes them much more conspicuous than deer) and is a likely reason for the overall larger group size of elk than deer (Fig. 1). However, a principal disadvantage of large group size is that competition for access to forage is greater within large groups than within small groups (Jarman 1974). Thus, the seasonal pattern of fluctuation in average group size is consistent with changes in forage quality and quantity during the period May through August. During June, elk and deer were surrounded by an abundance of high quality forage; hence, within-group competition for forage resources presumably was relatively low, even within large groups. However, as the season progressed and forage quality decreased, within-group competition probably increased as animals were increasingly selective about what bites to take while foraging. As a consequence, average group size decreased. The increase in average group size observed at the end of the season probably was due to an increasing concentration of animals foraging in local habitat patches where plant phenology (dessication at that time) was slightly delayed relative to average conditions in the study area. Therefore, the decrease in group size during July and August for elk, and July through September for deer, may have reflected an increased selectivity for individual plants during foraging, whereas the increase in group size in October reflected an increased selectivity for microhabitat patches. The large groups observed

in October, therefore, were presumably a consequence of habitat patchiness rather than any benefit of large group size. This explanation for increasing group size during fall also has been suggested for Rocky Mountain mule deer (*O. h. hemionus*) (Mackie 1970:28).

The elk rutting period occurred during September and lasted into October (deer did not rut until November). Breeding behavior may tend to increase group size as bulls and cows form harems (Darling 1937), and this tendency may explain the increase in elk group size during September and the decrease in deer group size. However, the difference in type of forage exploited by elk and deer also may have been responsible for the observed differential change in group size. Since I do not have data for comparisons of microhabitat patches, my explanation can only be speculative. However, I suggest that the increase in elk group size during September was attributable primarily to increased microhabitat patchiness of forage resources being exploited by elk. Quantity and quality of herbaceous vegetation was decreasing rapidly, and the benefits of finding local patches of vegetation where phenology was slightly delayed would have been substantial.

Elk and deer spent about half their time harvesting food and half their time processing it (Table 1). For the most part, traveling occurred at the same time as foraging; only occasionally did animals travel without foraging. These data are very similar to data reported by others (Craighead *et al.* 1973, Collins *et al.* 1978).

TABLE 1. Average daily activity regimes of elk and deer.

	Percent of time			
	Ruminating/ resting	Foraging	Traveling	Other activity
Elk	42.0	55.3	2.3	0.4
Deer	42.3	54.3	2.3	1.1

The observed daily activity pattern (Fig. 2), with peaks of activity occurring around dawn and dusk, is characteristic of deer (Dasmann and Taber 1956) and elk (Craighead *et al.* 1973) and probably is related to daily fluctuations in the thermal environment (Dasmann and Taber 1956). The seasonal activity pattern (Fig. 3), however, probably is related to seasonal fluctuations in forage quality and quantity. As forage quality decreased through the second half of the summer, the percentage daily activity increased as animals presumably were increasingly selective about the plant individuals or parts they consumed. For both elk and deer, activity apparently peaked at the latest time when increased searching effort (per bite) still yielded a gain in terms of forage quality. In September for elk and October for deer, forage quality apparently had decreased to the point where increased food processing time (resulting from slower rumen turnover rates) approached the time available for harvesting, and percentage activity dropped. The difference in seasonal activity peaks (August for elk, September for deer) corresponded with the differences in group size observed in August and September. By September, elk foraging strategy presumably had shifted emphasis from plant individuals to microhabitat patches; this shift presumably did not occur until October for deer.

The effects of seasonal fluctuations in forage quality can be seen more clearly in

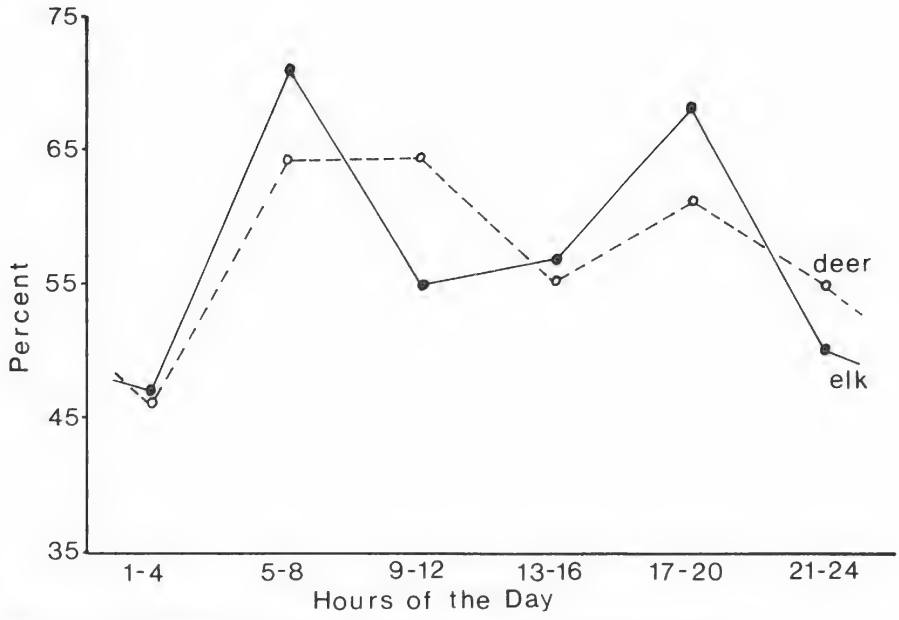


Figure 2. Daily patterns of percentage activity (percentage of time spent active).

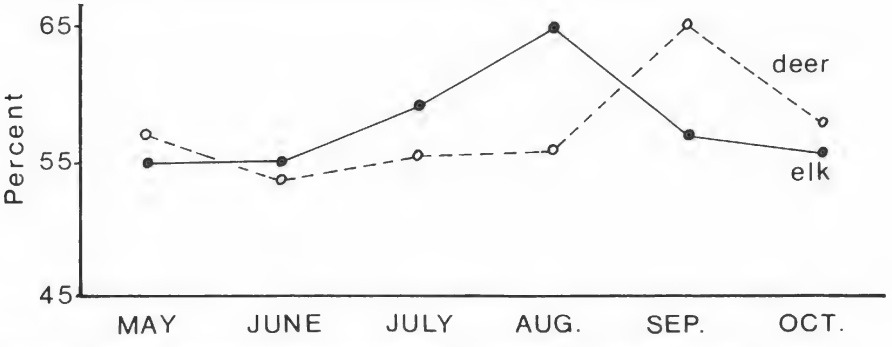


Figure 3. Seasonal patterns of percentage activity (percentage of time spent active).

the patterns of activity/inactivity duration (Figs. 4 and 5). During June, when forage quality was at its peak, periods of food harvesting (activity) and processing (inactivity) were short. Foraging animals readily filled their rumens to capacity with high quality forage; the high quality forage digested rapidly; and rumen turnover rates were high. The latter is consistent with data on voluntary intake and rumen turnover rate relationships (Van Soest 1965). As forage quality decreased with the passage of time, longer periods were required to reach rumen fill, presumably because animals were being increasingly selective about plant parts or individuals. Nevertheless, diet quality decreased; rumen turnover rate decreased; and duration of a food processing period increased.

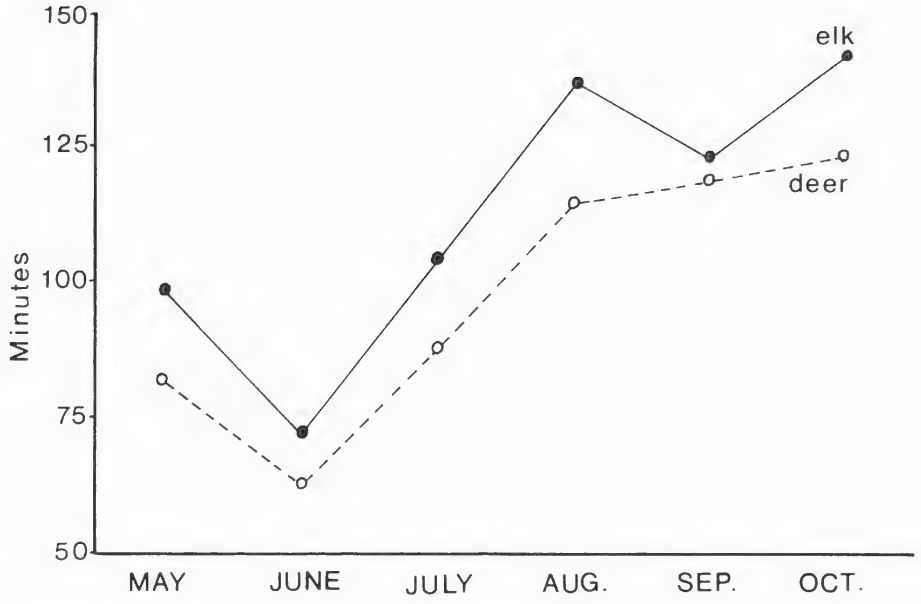


Figure 4. Seasonal patterns of average duration (minutes) of periods of activity.

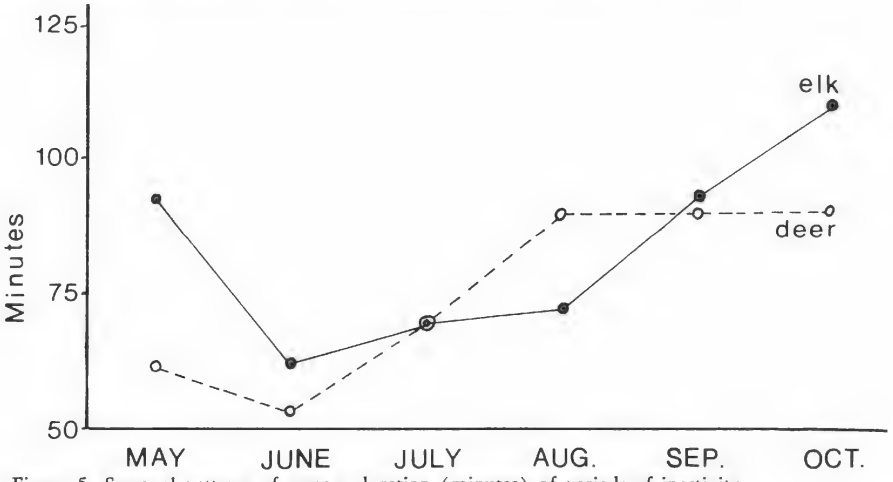


Figure 5. Seasonal patterns of average duration (minutes) of periods of inactivity.

The decrease in duration of foraging bouts that occurred in September for elk may, perhaps, have been associated in some way with the rut. However, it may also have been associated with a shift in foraging strategy from emphasis on individual plants to emphasis on microhabitat patches. Diet quality continued to decline (as evidenced by duration of inactivity periods), but less time was spent searching per individual bite; hence, rumen fill was attained in less time per foraging bout.

Travel distance (Fig. 6) was least during May, when green-up and forage avail-

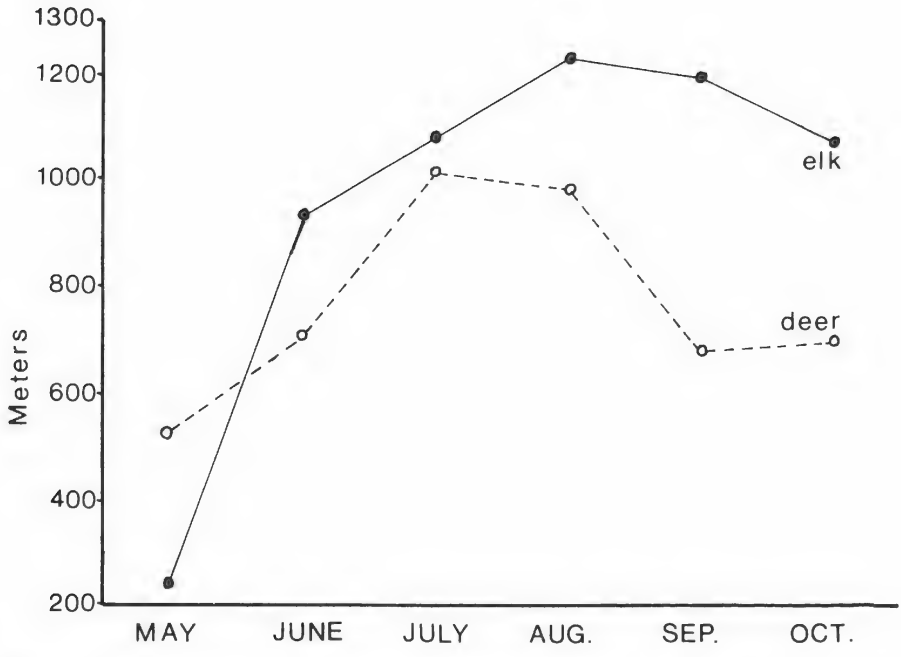


Figure 6. Seasonal patterns of distance traveled (meters traveled during a 24 hr day).

ability was restricted to the patches of habitat that were first clear of snow. Travel distance increased in June as high quality forage was widely and abundantly distributed. This might be a time when animals could traverse their home range and refamiliarize themselves with the distribution of forage resources without suffering any costs in terms of diet quality. As forage quality declined, and search effort increased, travel distance increased and then decreased. The increase in travel distance seemingly resulted from increased selectivity of plant individuals. The decrease in travel distance could be attributable to a shift in emphasis from individual plants to microhabitat patches by elk. A shift in emphasis from individual plants to specific portions of shrubs (i.e., a shift in emphasis from searching for current year growth from many individuals to searching for younger branches on fewer individuals) may have occurred in September for deer and may have been followed in October by a shift in emphasis to microhabitat patches.

The fairly similar daily travel distances but grossly different home range sizes (1873 ha for the elk, 241 ha for the deer) are important, because they indicate the scale at which these animals viewed their habitat. Deer traveled from plant to plant within a relatively small home range, whereas elk traveled from mesic habitat patch to mesic habitat patch within a relatively large home range. The differing home ranges can probably be attributed to differences in forage classes consumed (shrubs and forbs vs. graminoids and forbs) and differences in the effects of mouth size on utilized plants. Animals with small mouths (especially browsers) tend to take individual bites and leave a substantial portion of a plant unutilized. On the other hand, animals with

large mouths (especially grazers) tend to harvest entire, or nearly entire plants (Jarman 1974), thus necessitating longer time intervals between periods of utilization for forage resources to recover.

The preceding interpretations of the seasonal patterns of temporal and spatial habitat use indicate that food harvesting and processing were the major determinants of elk and deer activity. Of particular interest is the similarity in the values of all activity parameters for both elk and deer, indicating that the daily and seasonal constraints on habitat use were very much the same for both species and that both species reacted to these constraints similarly. The preceding interpretations of the data are speculative; they suggest a seasonal shift in foraging emphasis from plant individuals and/or parts to microhabitat patches which result from differences in slope exposure, local shading, or variations in soil moisture conditions (Fig. 7). Finding microhabitats where phenology is delayed relative to average conditions tends to delay and dampen the effect of phenological change on forage quality. In June, when forage quality and quantity are relatively great in all microhabitats, the best foraging strategy is selection

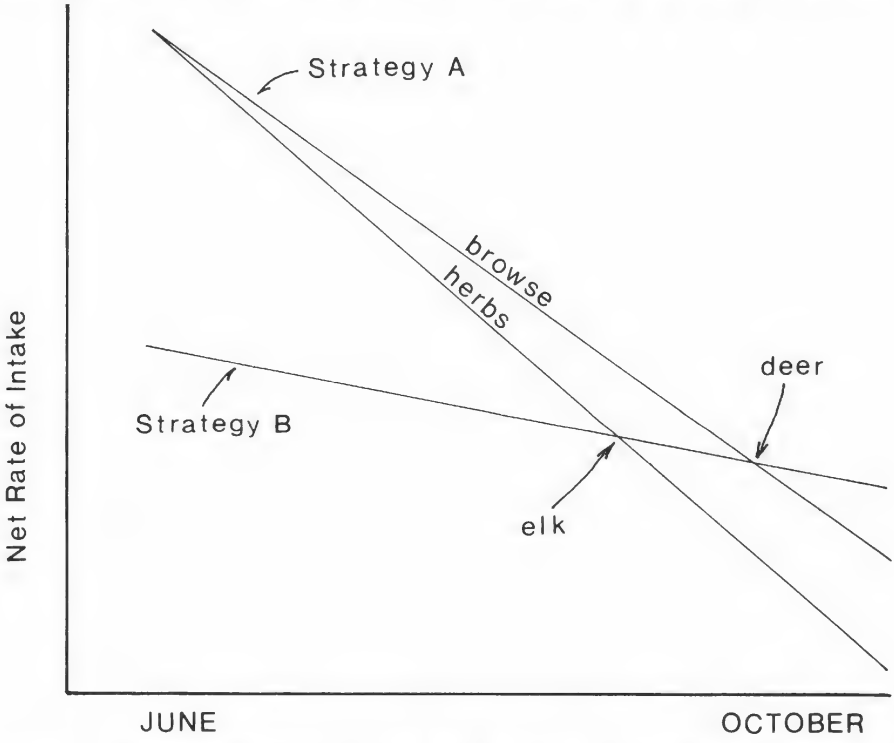


Figure 7. Graphical representation of nutrient intake rate effects of two foraging strategies differing in emphasis on selection. The net rate of nutrient intake declines with the passage of time as a consequence of changes in plant phenology. Strategy A emphasizes selection of individual plants; Strategy B emphasizes selection of microhabitat patches where plant phenology is delayed relative to average conditions. The optimal choice of strategies switches at their point of intersection. Although the actual curves probably are not linear, the essential points are the same for both linear and reasonable curvilinear relationships: 1) the curves of strategies A and B intersect toward the end of the growing season, and 2) the intersection occurs earlier for elk than for deer.

of individual plants. However, by October, plant phenology is greatly advanced, and "green" forage is available only in microhabitat "pockets" where phenology is delayed; hence, the best foraging strategy at this time is selection of microhabitat patches. Since the quality of herbaceous forage declines more rapidly than browse quality (Hanley 1980), the shift in foraging strategies should occur earlier in the season for elk (primarily grazers) than for deer (primarily browsers).

Of course, the strength and generality of these conclusions are limited because the temporal and spatial patterns of activity were based on data collected from only two animals and that the presumed seasonal shift in foraging emphasis is speculative. Other data are needed to test whether such a shift actually occurs. Nevertheless, the patterns reported here are interesting and suggestive of generality. While the data do not constitute a test of any hypothesis, they do offer some empirical support of the hypothesis that foraging constraints dominate the daily activity budget of female deer during spring through fall.

Literature Cited

Collins, W. B., P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. J. Wildl. Manage. 42:799-810.

Craighead, J. J., F. C. Craighead, Jr., R. L. Ruff, and B. W. O'Gara. 1973. Home Ranges and Activity Patterns of Nonmigratory Elk of the Madison Drainage Herd as Determined by Biotelemetry. Wildl. Monogr. 33.

Darling, F. F. 1937. A Herd of Red Deer. Oxford Univ. Press, London.

Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. J. Mammal. 37:143-164.

Estes, D. D. 1974. Social organization of the African bovidae, *in* V. Geist and F. Walther (eds.) The Behaviour of Ungulates and Its Relation to Management. Vol. 1. Inter. Union Conserv. Nature Pub. No. 24. Inter. Union Conserv. Nature, Morges, Switzerland.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. United States Dept. Agric. Forest Service Gen. Tech. Rept. PNW-8.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. Amer. Zool. 14: 205-220.

Hanley, T. A. 1980. Nutritional Constraints on Food and Habitat Selection by Sympatric Ungulates. Univ. Wash., Seattle, Ph.D. thesis.

Hungate, R. E. 1966. The Rumen and Its Microbes. Academic Press, New York and London.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48(3-4):215-267.

Mackie, R. J. 1970. Range Ecology and Relations of Mule Deer, Elk, and Cattle in the Missouri River Breaks, Montana. Wildl. Monogr. 20.

Mitchell, B., D. McCowan, and I. A. Nicholson. 1976. Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*. J. Zool., Lond. 180:107-127.

Moen, A. N. 1973. Wildlife Ecology: An Analytical Approach. Freeman, San Francisco.

Schoen, J. W. 1977. The Ecological Distribution and Biology of Wapiti (*Cervus elaphus nelsoni*) in the Cedar River Watershed, Washington. Univ. Wash., Seattle, Ph.D. thesis.

Short, H. L. 1981. Nutrition and metabolism, pp. 99-127 *in* O. C. Wallmo (ed.) Mule and Black-tailed Deer of North America. Univ. Neb. Press, Lincoln.

Tester, J. R., S. W. Warner, and W. W. Cochran. 1964. A radio-tracking system for studying movements of deer. J. Wildl. Manage. 18:42-45.

Van Soest, P. J. 1965. Symposium on factors influencing the voluntary intake of herbage by ruminants: voluntary intake in relation to chemical composition and digestibility. J. Anim. Sci. 24:834-843.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30:122-127.

Received August 18, 1980
Accepted for publication March 1, 1981

Randall L. Gresens

Department of Geological Sciences
University of Washington
Seattle, Washington 98195

Early Cenozoic Geology of Central Washington State: I. Summary of Sedimentary, Igneous, and Tectonic Events

Abstract

New field mapping and radiometric dating have made possible the construction of a detailed geologic history for early Cenozoic rocks of central Washington. The lower Eocene Swauk Formation was apparently a widespread unit consisting primarily of fluvial arkosic sandstone; it was folded about E-W axes prior to extrusion of the middle Eocene Teanaway Basalt. NE-trending Teanaway dikes are coeval with the NW-trending bimodal Corballey Canyon dike swarm located only 50 km away. The NW-trending Chiwaukum graben was active over about a 6 my span during middle Eocene time, and at least 5800 m of Chumstick Formation accumulated in it. The Chumstick is dominantly fluvial arkosic sandstone with interbedded tuff, but the upper part is a shaly lacustrine facies. The region was tectonically and magmatically quiet during the late Eocene and early Oligocene and was beveled to a surface of low relief mantled with deeply weathered bedrock. Two hundred and eighty meters of Wenatchee Formation, a dominantly fluvial unit of quartzose sandstone and shale with minor tuff beds, was deposited on the erosion surface. Compressional deformation within 5 my of its deposition involved the Wenatchee and older rocks in minor thrust faulting and folding. Hornblende andesite sills and dikes of the Horse Lake Mountain complex intruded all sedimentary units in the southern part of the graben in late Oligocene time; their emplacement was synchronous with deformation by NW-trending right-lateral shearing. Bentonitic shales of Miocene age were deposited prior to extrusion of the Columbia River Basal Group.

Introduction

The Chiwaukum graben and adjacent areas (Fig. 1) encompass a wealth of geologic relationships that are critical to understanding the geologic history of central Washington during the early Cenozoic. Part I of this report introduces new radiometric dates, summarizes old dates, and reviews the sedimentary, igneous, and tectonic history from Paleocene through Miocene time. Part II discusses the implications for plate tectonics and delineates some of the unsolved tectonic problems.

Recent work has redefined the stratigraphy of diverse sedimentary units that were previously included under the term "Swauk Formation" (Gresens *et al.* 1981). For convenience, the Chiwaukum graben, a major NW-trending structure, is used as a reference area, and the stratigraphy is divided into three parts: the graben interior and contiguous terranes to the SW and NE (Fig. 2).

Geologic History

The early- to mid-Cenozoic history of the Chiwaukum graben and vicinity is summarized in Table 1. The tripartite division used for the stratigraphic summary is retained. The positions of the Entiat and Leavenworth faults, which bound the graben, respectively, on the east and west, are used to divide the region, even though they did not come into existence until post-Teanaway time.

Eocene Events

South of the Mt. Stuart massif, in the area SW of the graben, the Swauk Formation

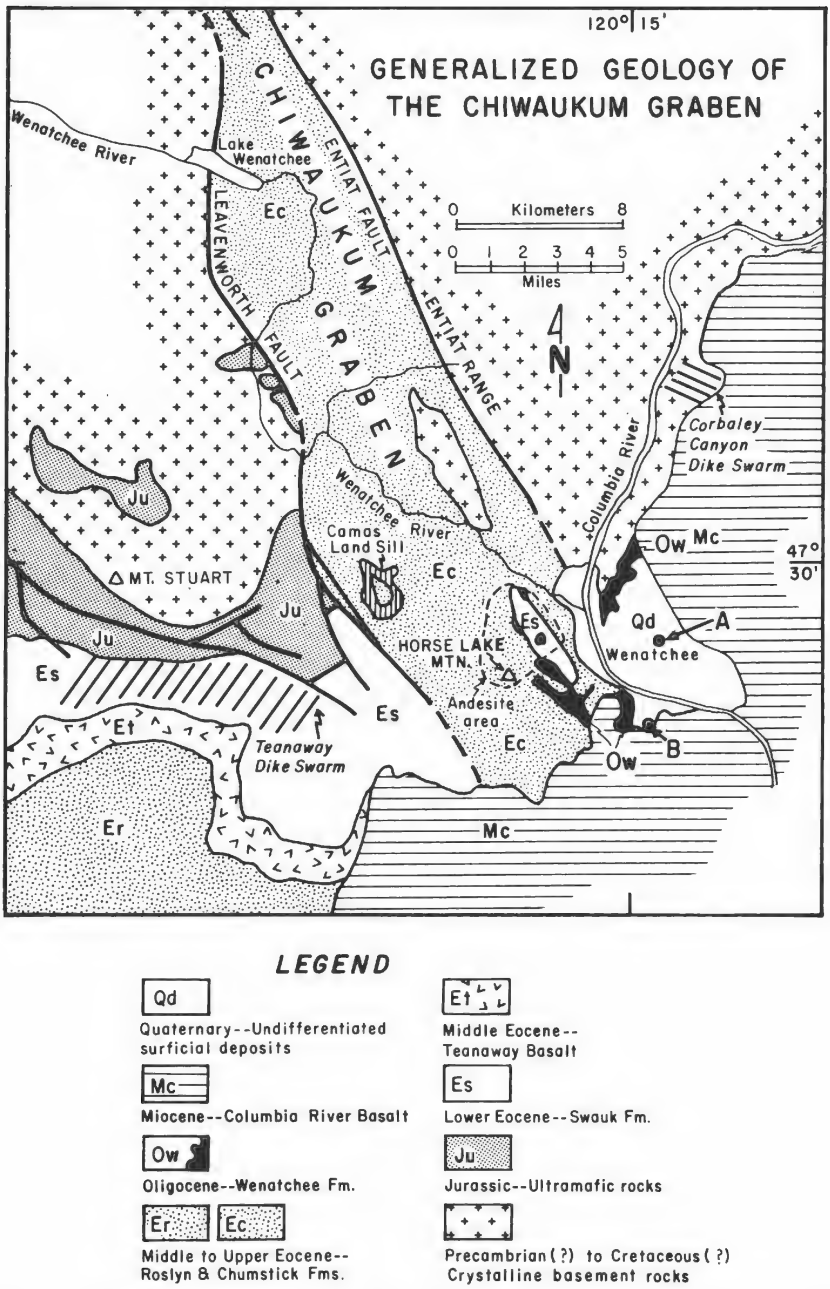


Figure 1. Generalized geology of the Chiwaukum graben in central Washington. The area outlined as "andesite area" (the Horse Lake Mountain complex) is shown in more detail in Fig. 5.

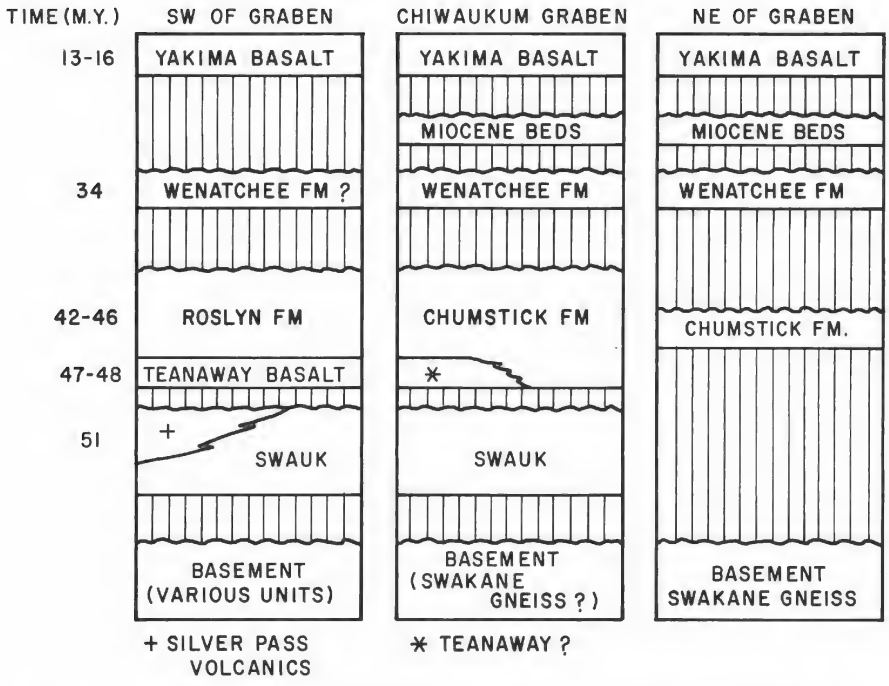


Figure 2. Stratigraphic columns for terranes within the Chiwaukum graben and on either side of it.

rests unconformably on crystalline rocks. Its basal section contains ironstones that are interpreted as diagenetically altered laterites developed on underlying sepentinite (Lupher 1944, Lamey and Hotz 1951). The upper Swauk Formation is reported to interfinger with the 51-my-old Silver Pass volcanics (Tabor and Frizzell 1977). The lower age is not known but could extend into the Paleocene. The Swauk, which consists mostly of fluvial and lacustrine arkosic sandstone and shale, was probably a widespread depositional unit and is at least 2300 m thick near the type locality (Frizzell 1979). The Swauk is probably correlative with the Chuckanut Formation exposed in the northern Puget Sound region west of the Cascade Range. Both the Swauk and Chuckanut contain abundant fossil palmetto leaves, which are not found in either the Chumstick or Roslyn Formations. Although these fossils are not diagnostic of age, they reflect differences in climate. Frizzell (1979) suggested correlation of Swauk and Chuckanut based on sandstone petrology. Although no Swauk Formation has been observed in the terrane NE of the graben, it may be absent because of subsequent erosion, rather than because of nondeposition, or it may be offset by the Entiat fault (Gresens, in press).

The Swauk was folded prior to deposition of Teanaway Basalt; folds have a general E-W trend (Tabor and Frizzell 1977), indicating N-S compression (Gresens 1979, Ewing 1980). This deformation took place between about 51-47 mybp. In contrast, the belt of Swauk Formation within the graben, exposed in the core of Eagle Creek

TABLE 1. Summary of geologic history of the Chiwaukum graben.

Time (m.y.)	Southwest of Graben	Leavenworth Fault / Chiwaukum Graben	Entiat Fault / Northeast of Graben
15-29	Regional Miocene deposition, including Columbia River Basalts, followed by uplift and erosion, involving ancestral Cascade Range		
29		Intrusion of Horse Lake Mountain Complex—hornblende andesite	
29-34		Folding and thrusting of Wenatchee Formation—NE-SW compression	
34		Deposition of Wenatchee Fm	
34-40(?)	←——Regional period of tectonic and magmatic quiescence——→		
40(?)-42(?)		Folding of Chumstick Formation—possible NE-SW compression	
42(?)-46(?)	Deposition of Roslyn Formation conformably on Teanaway Basalt	Deposition of Chumstick Formation in subsiding Chiwaukum graben—NE-SW extension	Active erosion of highland area Local deposition of Chumstick Formation
46(?)		Initiation of the Chiwaukum graben—NE-SW extension	
47-48	Emplacement of Teanaway dike swarm in Swauk Formation and extrusion of Teanaway Balsalt unconformably over Swauk Formation—WNE-ESE extension		Emplacement of Corbaley Canyon dike swarm (rhyodacite) into Swakane Gneiss—NNE-SSW extension
47-51	Folding of Swauk Formation—N-S compression		
51-??	Regional deposition of Swauk Formation		??????

anticline near the city of Wenatchee, has the same NW structural grain as the trends of the Leavenworth and Entiat faults and the anticline. Evidence of multiple folding, timing unknown, is present in these rocks.

The age of the Teanaway Basalt is about 47 my based on whole-rock K-Ar ages (R. W. Tabor, pers. comm., 1981). An extensive swarm of basalt dikes, feeders of Teanaway volcanism, cuts the Swauk Formation in the terrane SW of the graben (Foster 1958, Southwick 1966). The dikes have a general orientation of about N15E and are nearly vertical (Foster 1958), which indicates WNW-ESE crustal extension during Teanaway time. Although the composition of the Teanaway is primarily basaltic, minor rhyolite occurs at the top of the unit (Clayton 1973).

A remarkable dike swarm also is present in the terrane NE of the graben. The dikes form prominent ridges where they are differentially weathered with respect to the metamorphic rocks (Fig. 3). They are well exposed in road cuts in Corbaley Canyon along U.S. Highway 2 and to the northwest along strike in road cuts on the west side

Figure 3. View of roadcuts in Corbaley Canyon. The felsic dikes weather differentially relative to the gneiss they intrude, and they show up in striking relief.

of the Columbia River. The dikes are dated at about 47-48 mybp; thus, they are at least broadly coeval with Teanaway volcanism. Corbaley Canyon dikes are bimodal but are dominated by felsic varieties ranging from porphyritic dacite to rhyolite with bipyramidal quartz phenocrysts (Waters 1926). Mafic rocks include both andesitic varieties and hornblende gabbros. The dikes are clearly pull-apart structures, and one exposure along the highway shows an intrusion of a second dike with chilled borders into an early dike that had been tensionally split apart (Fig. 4). The dikes have a strong N70W trend, which indicates NNE-SSW crustal extension during their emplacement. Other dike swarms, part of the broad period of Challis-Absaroka volcanism (Armstrong 1978), are common throughout the region to the north and northwest of the Corbaley Canyon swarm.

Initiation of the Chiwaukum graben as an active structure probably began about 46 mypb, based on the age of the Chumstick Formation. During its subsidence, it accumulated a thick (5800 m), mainly fluvial and alluvial, sequence of arkosic sandstone and shale (Chumstick Formation) (Whetten 1977; Gresens *et al.*, in press). Toward the end of its activity, sedimentation was dominated by shaly lacustrine facies as reflected in the upper Chumstick Formation (Nahahum Canyon member) (Whetten 1977). Dating of the Chumstick, and hence of graben activity, is based on a suite of nine fission-track ages from interbedded tuff units that range from 41.9 to 48.8 mybp (Whetten 1977; Gresens *et al.*, in press). Because of analytical uncertainty in the fission-track method, there is significant variance of the age of the sample population, but the active life of the graben probably spanned the range from about 40 to 46 mybp.

Along the Leavenworth fault zone in the southern half of the graben, there is an occurrence of chaotic basalt fragment interbedded with the Chumstick Formation. Tabor and Frizzell (1977, Frizzell and Tabor 1977) have interpreted this as a Teanaway

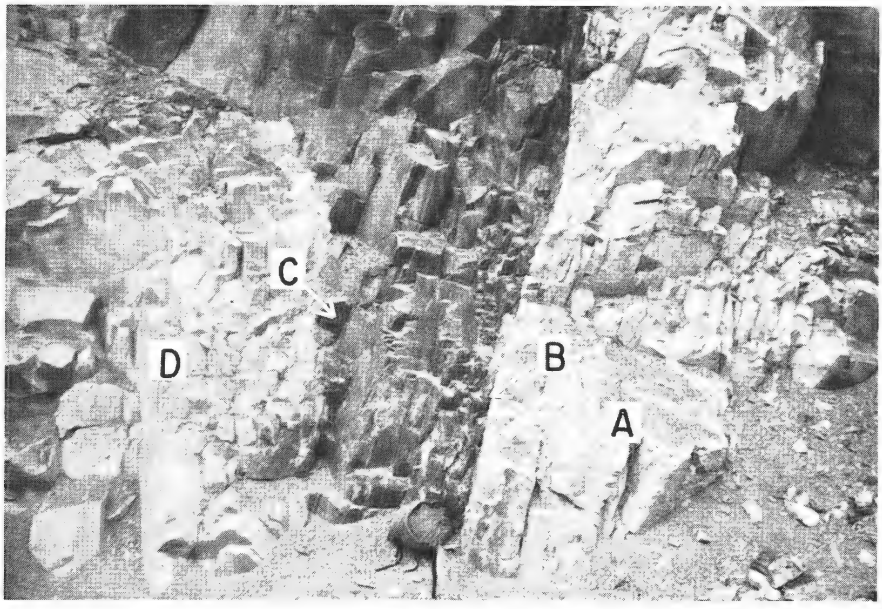


Figure 4. A tensional dike-within-a-dike structure along roadcut in Corbaley Canyon. "A" is the older dike that contacts gneiss to the immediate right of the photo. "B" is the sharp chilled margin of the inner (younger) dike against the outer dike; the composition of the margin is more mafic than the main part of either dike, as indicated by the darker color. "C" is the gradational contact of the chilled margin into the main part of the inner dike. "D" is the main interior part of the inner dike; although "D" is felsic like "A," the two dikes are texturally distinct. The mirror image of the relationships shown in the photo occur to the immediate left of the photo. Rucksack indicates scale.

volcanic breccia. They thus have inferred that deposition of the Chumstick and initiation of graben subsidence pre-date the Teanaway Basalt. The writer has seen the locality and reserves final judgment. However, thick conglomerates with well-rounded clasts, composed nearly exclusively of basalt, occur nearby in blocks of lower Chumstick faulted upward along the Leavenworth fault zone. These must be fanglomerates shed from the Teanaway Formation into the subsiding graben, similar to serpentinite fanglomerates described by Cashman and Whetten (1976) farther north along the Leavenworth fault. It is possible that the chaotic basalt fragments are associated mass-wasting deposits (perhaps debris flows) shed into the graben from pre-existing Teanaway Formation perhaps a million or more years after its extrusion, rather than volcanic breccia coeval with Teanaway extrusion.

The Chiwaukum graben was flanked by highlands of crystalline basement rock during deposition of Chumstick Formation (Whetten 1977, Buza 1979). Apparently the terrane east of the Entiat fault was a persistent highland. The terrane west of the Leavenworth fault was only an intermittent highland, and the Chumstick may have been locally continuous with the Roslyn Formation lying to the west over regions that were subjected to later erosion. The Roslyn Formation has a thickness estimated as 1900 m (Bressler 1951). Its equivalent within the graben, the Chumstick Formation, is much

thicker; Whetten (1977; Gresens *et al.*, in press) estimated it conservatively at 5800 m. Based on the evidence by Buza (1979) and Whetten (1977) and the continuation of Whetten's structural and stratigraphic patterns to the SE, Gresens (1980) argued that Chumstick Formation lying east of the Entiat fault was emplaced by post-34 mybp thrusting out of the graben. Although this interpretation is supported by structural data and remains valid for Chumstick exposures relatively near the Entiat fault, additional fieldwork has revealed poorly exposed Chumstick sufficiently far east of the Entiat fault that it is probably in its original depositional position (Fig. 1). Thus the Entiat highland, although probably tectonically active continually during Chumstick time, may have been breached by valleys that passed into adjacent depositional basins now covered by the Columbia River Basalt Group.

It is necessary to assign at least a component of NE-SW crustal extension to the Chiwaukum graben during its active stage. Table 1 indicates (with some uncertainty) a possibility of NE-SW compression toward the waning stages of Chumstick deposition. This is based on the recognition of NW-trending folds in the Chumstick (including the major Eagle Creek anticline) as well as minor NW-trending thrust faults (Whetten and Laravie 1976). However, Whetten (1977) and Buza (1979) believe that a bedrock horst was present in the graben during Chumstick deposition at the site now occupied by the Eagle Creek anticline. It is possible that the Eagle Creek structure is a faulted drape fold over the horst and was produced during extension of the graben, rather than by later compression. Smaller folds and thrust faults could have been produced by post-34 mybp compressive deformation. Thus the evidence does not demand a pre-Wenatchee period of compressive deformation, which would require a reversal of tectonic stress during the waning stages of graben activity. Minor intrusive igneous activity continued within the Chiwaukum graben during its waning stages, as indicated by K-Ar dates of 41-46 mybp on both mafic and felsic intrusive rocks.

Between 34-40(?) mybp, the region was in a period of tectonic and perhaps magmatic quiescence. The younger limit is well constrained by the age of the Wenatchee Formation, which rests with profound unconformity on all older units. The older limit has the uncertainty associated with the range of fission-track ages of the Chumstick Formation and the time necessary to deposit the Nahahum (upper) member, which lacks tuff beds. The period of quiescence and deep erosion coincides with the same phenomenon found over most of western North America (Coney 1971, 1972; Gresens 1978, 1980, in press) and is particularly well documented in the southern Rockies (Epis and Chapin 1975). It is considered to mark the end of Laramide deformation in western North America (Coney 1971, 1972). During this period, topography that existed in Chumstick time was destroyed by erosion.

Oligocene Events

The age of the Wenatchee Formation is defined by two precise fission-track dates averaging 34 mybp (Gresens *et al.*, in press); an Oligocene age also has been determined from palynological data (Newman 1977). The Wenatchee Formation is about 280 m thick and consists mainly of quartzose sandstone and partly tuffaceous shale and siltstone that are interpreted, respectively, as fluvial sand of braided stream complexes and associated overbank deposits (Gresens *et al.*, in press). At the end of the late Eocene-early Oligocene erosional episode, the area from central Washington

to the Puget Sound region must have been a relatively low-lying plain, perhaps with local monadnocks of more resistant rocks.[1]

The Chiwaukum graben was subjected to compressive deformation between 29 and 34 mybp (Gresens 1980). During this episode, Chumstick rocks were thrust out of the graben and across the trace of the Entiat fault along NE-directed thrust faults; for reasons of scale, they are not shown on Figure 1. The overlying Wenatchee was folded and faulted. The younger age limit is defined by the presence of hornblende andesite that intrudes a thrust plane in Wenatchee Formation but is not itself sheared. The total calculated shortening along the east side of the graben is only 2.5-3.0 km. This deformation documents NE-SW crustal compression. Minor thrust faults involving the Chumstick, mapped by Whetten and Laravie (1976) in the north end of the graben, could be related to this episode, but there are no narrow constraints on their age.

Intrusions of hornblende andesite (Horse Lake Mountain complex), mainly in the form of sills with associated dikes, are extensive in the southern part of the Chiwaukum graben. Most are exposed in rather monotonous Chumstick terrane, but some intrude the Wenatchee Formation near the eastern border of the graben. K-Ar ages from various sources give an average age of about 29 my.

The Horse Lake Mountain complex was described in part by Bayley (1965), who mapped many of the sills and dikes and examined their petrography. Complete mapping and interpretation of the complex is presented by Gresens.[2] The complex ranges in composition from basaltic andesite to andesite. A variety of textural types are represented, but many contain phenocrystic hornblende that ranges to several decimeters in longest axis. Many sills and dikes are altered to chlorite, zeolite, and calcite. Calcite partially replaces hornblende or plagioclase cores in some rocks.

A striking feature of the complex is the thin screens of undisturbed sedimentary rock, sometimes less than one meter thick, between numerous sills. Excellent exposures in some cliffs with 500 m of vertical exposure show sections that are made of greater than 50 percent igneous materials, yet the sedimentary beds show no signs of forceful emplacement.

Figure 5 shows a WNW-trending structure that appears to have cut across at least part of the Chiwaukum graben at about 29 mybp. The fault zone labeled "A" on Figure 5 is an old fault contemporaneous with graben activity. Fault "B" is a post-34 mybp fault that involves the Wenatchee Formation, but its possible relationship to fault zone "C" cannot be determined. At fault zone "C," a belt of Wenatchee Forma-

---

[1]Rocks of late Eocene age on the east side of the Puget Sound region are essentially coal-bearing arkosic sandstone (Tiger Mountain Formation) and volcano-genic and tuffaceous sandstone, siltstone, and shale (Tukwila Formation), both of continental origin (Vine 1969). The younger Renton Formation, which apparently is broadly coeval with the development of the late Eocene-early Oligocene erosion surface to the east, contains continental sandstones that are more quartz-rich, less plagioclase-rich, and more kaolinitic than the older units (Vine 1969). The uppermost (early Oligocene) part of the Renton Formation contains fossils diagnostic of brackish water. Within Puget Sound proper, there is an occurrence of marine rocks (the Blakely Formation) that are essentially coeval with the Renton Formation. These have been interpreted as a possible submarine fan complex (McLean 1977). The strand line during the late Eocene and early Oligocene thus must have been west of the Cascade Range and near the Puget Sound lowland. Transitional rocks deposited on the low-lying plain between the Wenatchee area and the old strand line have been removed by Cascade uplift and erosion.

[2]Map and bulletin for Wenatchee and Monitor 7½-min quadrangles in preparation for Division of Geology and Earth Resources, State of Washington.

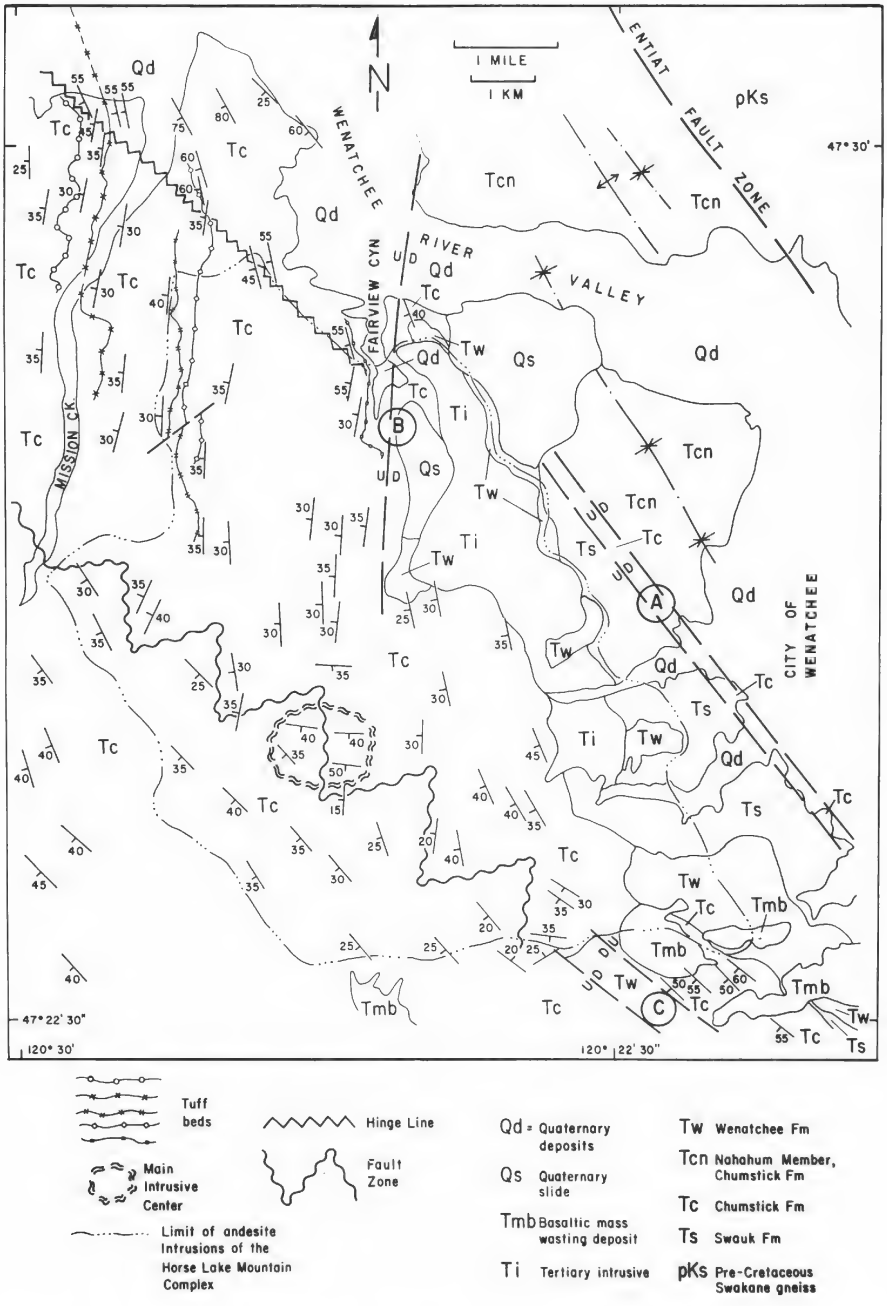


Figure 5. Structural detail of part of the southern Chiwaukum graben that contains the Horse Lake Mountain complex. Strikes and dips of parts of the Chumstick Formation are emphasized.

tion occupies a small graben in the Chumstick Formation, and the fault zone is thus post-34 mybp. The northwest projection of the fault zone cannot be directly mapped because of the lack of markers. However, a broad belt of disturbed beds marks the presumed projection of the fault zone. South of the fault zone, Chumstick bedding strikes NW, which is the general structural grain of the Chumstick Formation within the graben. North of the fault zone, the Chumstick bedding strikes uniformly north to slightly northeast. As this zone is followed north, the strikes swing back to the northwest through a hinge line. At four places along the line, individual tuff beds can be followed unbroken through the hinge. Angular unconformities between the Wenatchee and Chumstick Formations prove that Chumstick bedding was already titled prior to post-Wenatchee faulting. The structure shown here suggests deformation by an underlying right-lateral shear couple that has broken through the Chumstick beds to the south but only rotated them about a hinge line to the north. The intervening area has the appearance of a giant "kink band," in which the steeply dipping Chumstick beds were caught. The main center of intrusive activity of the 29-my-old hornblende andesites is within the fault zone, and some intrusions extend south of it into NW-striking Chumstick beds. But most of the intrusive activity is confined to the area within the giant "kink band," suggesting that tensional stretching within the band allowed contemporaneous passive intrusion of the many sills. One sill (not shown on the scale of Fig. 5) pinches out exactly at the hinge line. The igneous rocks apparently were intruded at shallow depth into sedimentary rocks saturated with carbonate-rich meteoric water. Deuteric alternation probably occurred soon after emplacement. The shear zone has not been mapped farther west.

Miocene Events

Continental sedimentation occurred at least locally prior to deposition of the Columbia River Basalt Group, as evidenced by unnamed Miocene rocks underlying basalt near the town of Malaga at sec. 6, T21N, R21E and sec. 31, T22N, R21E (Gresens *et al.*, in press) (Fig. 1). These beds are about 50 m thick and are composed primarily of bentonitic shale with minor sand stringers and thin carbonaceous interbeds probably derived from humic material. The unit probably represents shallow swampy lakes or over-bank deposits. Structurally and stratigraphically, the unit near Malaga is positioned between Wenatchee Formation and younger Columbia River Basalt Group. Preliminary palynological data (Estella Leopold, pers. comm., 1978) suggest that the age is Miocene.

In the area SW of the graben, an unnamed unit has a stratigraphic position between the Roslyn Formation and the Columbia River Basalt Group. The generally poor exposure in roadcuts along the Teanaway River drainage do not permit diagnostic assignment of the unit to Wenatchee Formation or to a unit of Miocene age at the time of this writing.

The Wenatchee Formation was eroded before deposition of the Columbia River Basalt Group, and the thinning is progressively greater from east to west (Gresens 1980). It is not possible to obain a definitive tectonic interpretation from the scanty data, but the observation would be consistent with the beginning of the present N-S trend of the modern Cascade Range uplift between 34-15 mybp. Similarly, it is not possible to state whether the Miocene beds near Malaga were of significantly greater

extent and were stripped along with the underlying Wenatchee Formation. It is possible that they are in part the erosional debris of the stripped Wenatchee Formation; the Wenatchee contains red oxidized siltstone that could be the source for red shales in the Miocene unit.

The geologic record of this area ends with outpouring of the Columbia River Basalt Group. These Miocene basalts and the post-basalt history are not discussed; the reader is referred to Loeschke (1979).

Literature Cited

Armstrong, R. L. 1978. Cenozoic igneous history of the U.S. cordillera from lat. 49°N, pp. 265-292 *in* Smith, R. B., and G. P. Eaton (eds.). Cenozoic Tectonics and Regional Geophysics of the Western Cordillera. Geol. Soc. Amer. Mem. 152.

Bayley, E. P., Jr. 1965. Bedrock Geology of the Twin Peaks Area, an Intrusive Complex near Wenatchee, Washington, Univ. Washington, M.S. thesis.

Bressler, C. T. 1951. The Petrology of the Roslyn Arkose, Pennslyvania Sta. Coll., Ph.D. thesis.

Buza, J. W. 1979. Dispersal patterns and paleogeographic implications of lower and middle Tertiary fluviatile sandstones in the Chiwaukum graben, east-central Cascade Range, Washington, pp. 63-73 *in* Armentrout, J. M., M. R. Cole, and H. TerBest, Jr. (eds.). Cenozoic Paleogeography of the Western United States. Soc. Economic Paleontologists & Mineralogists, Pacific Sec.

Cashman, S. M., and J. T. Whetten. 1976. Low-temperature serpentinization of peridotite fanglomerate on the west margin of the Chiwaukum graben, Washington. Geol. Soc. Amer. Bull. 87: 1773-1776.

Clayton, D. N. 1973. Volcanic History of the Teanaway Basalt, East-Central Cascade Mountains, Washington. Univ. Washington, M.S. thesis.

Coney, P. J. 1971. Cordilleran tectonic transitions and motion of the North American plate. Nature 233: 462-465.

———. 1972. Cordilleran tectonics and North America plate motion. Am. Jour. Sci. 272: 603-628.

Epis, R. C., and C. E. Chapin. 1975. Geomorphic and tectonic implications of the post-Laramide, late Eocene erosion surface in the southern Rocky Mountains, pp. 45-74 *in* Curtis, B. F. (ed.). Cenozoic History of the Southern Rocky Mountains. Geol. Soc. Amer. Mem. 144.

Ewing, T. E. Paleogene tectonic evolution of the Pacific Northwest. Jour. Geology 88: 619-638.

Foster, R. J. 1958. The Teanaway Dike Swarm of central Washington. Am. Jour. Sci. 256: 644-653.

Frizzell, V. A., Jr. 1979. Petrology and stratigraphy of Paleogene nonmarine sandstones, Cascade Range, Washington. U.S. Geol. Survey Open-File Rept. 79-1149.

———, and R. W. Tabor. 1977. Stratigraphy of Tertiary arkoses and their included monolithologic fanglomerates and breccias in the Leavenworth fault zone, central Cascades, Washington (abs.). Geol. Soc. Amer., Abstracts with Programs 9: 421.

Gresens, R. L. 1978. Regional significance of a late Eocene/early Oligocene erosion surface exposed in central Washington State (abs.). Geol. Soc. Amer., Abstracts with Programs 10. 107.

———. 1979. Timing of Cenozoic igneous and tectonic events on the eastern flank of the Cascade Range in central Washington (abs.). Geol. Soc. Amer., Abstracts with Programs II: 80.

———. 1980. Deformation of Wenatchee Formation and its bearing on the tectonic history of the Chiwaukum graben, Washington, during Cenozoic time. Geol. Soc. Amer. Bull. 91: 4-7 (Part I), 115-155 (Part II).

———. In press. Extension of the Telluride erosion surface to Washington State, and its regional and tectonic significance. Tectonophysics.

———. In press. Early Cenozoic geology of central Washington State. II. Implications for plate tectonics and alternatives for the origin of the Chiwaukum graben. Northw. Sci.

———, C. W. Naeser, and J. T. Whetten. Stratigraphy and age of the Chumstick and Wenatchee Formations: Tertiary fluvial and lacustrine rocks, Chiwaukum graben, Washington. Geol. Soc. Amer. Bull. 92: 233-236 (Part I), 841-875 (Part II).

Lamey, C. A., and P. E. Hotz. 1951. The Cle Elum River nickeliferous iron deposits, Kittitas County, Washington. U.S. Geol. Survey Bull. 978-B: 27-67.

Loeschke, Jörg. 1979. Basalts of Oregon (U.S.A.) and their geotectonic environment. I. Petrochemistry of Tertiary basalts of the Oregon Coast Range. N. Jb. Miner. Abh. 134: 225-247.

Lupher, R. L. 1944. Stratigraphic aspects of the Blewett-Cle Elum iron ore zone, Chelan and Kittitas Counties, Washington. Washington Div. Mines and Geol. Rept. Inv. 11.

McLean, Hugh. 1977. Lithofacies of the Blakely Formation, Kitsap County, Washington—a submarine fan complex?. Jour. Sed. Pet. 47: 78-88.

Newman, K. R. 1977. Palynologic biostratigraphy of some early Tertiary nonmarine formations in central and western Washington (abs.). Geol. Soc. Amer., Abstracts with Programs 9: 1113.

Southwick, D. L. 1966. Petrography, chemistry, and possible correlations of the Camas Land Sill and Teanaway Dike Swarm, central Washington. Northw. Sci. 40: 1-16.

Tabor, R. W., and V. A. Frizzell, Jr. 1977. Tertiary stratigraphy of the central Cascades Mountains, Washington State. Part II. Stratigraphy of the Swauk, Silver Pass, Teanaway, and Roslyn Formations, pp. 88-100 *in* Brown, E. H., and R. C. Ellis (eds.). Geological Excursions in the Pacific Northwest. Bellingham, Western Washington Univ. Press.

Vance, J. A. 1977. Fission track geochronology of the Tertiary volcanic rocks of the central Cascade Mountains, Washington (abs.). Geol. Soc. Amer., Abstracts with Programs 9: 250.

———. 1979. Early and middle Cenozoic arc magmatism and tectonics in Washington State (abs.). Geol. Soc. Amer., Abstracts with Programs 11: 132.

Vine, J. D. 199. Geology and coal resources of the Cumberland, Hobart, and Maple Valley quadrangles, King County, Washington. U.S. Geol. Survey Prof. Pap. 624.

Waters, Aaron, 1926. The Petrography of Corbaley Canyon. Univ. Washington, B.S. thesis.

Whetten, J. T. 1977. Tertiary stratigraphy of the central Cascades Mountains, Washington State. Part III. Rocks of the Chumstick Creek and Nahahum Canyon areas, pp. 100-09 *in* Brown, E. H., and R. C. Ellis, (eds.). Geological Excursions in the Pacific Northwest. Bellingham, Western Washington Univ. Press.

———, and J. A. Laravie. 1976. Preliminary geologic map of the Chiwaukum 4 NE quadrangle, Chiwaukum graben, Washington. U.S. Geol. Surv. Misc. Field Studies Map MF-794, scale 1:24,000.

Received May 20, 1981
Accepted for publication July 17, 1981

David B. Costain[1]

and

B. J. Verts

Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331

Age Determination and Age-Specific Reproduction in Belding's Ground Squirrels

Abstract

Numbers of densely stained lines in mandibles of more than 95 percent of marked Belding's ground squirrels (*Spermophilus beldingi*) corresponded with their known ages or known minimum ages; seemingly, one new line was formed each year, and evidence of resorption of lines was absent. Mean litter sizes, based on counts of embryos or pigmented sites of implantation, for 273 females collected in 1975 and 1976 on the Oregon State University Harris Ranch, Grant County, Oregon, and 311 females obtained from hunters during the same year on the adjacent Izee Ranch, increased with age in five of six samples. Mean litter sizes were significantly larger among 2-year-old squirrels than among 1-year-olds in five of six samples but were not significantly larger than among 3-year-olds in three of five samples. Because few squirrels had three densely stained lines and none had four or more, and because differences in mean litter sizes between second-cohort and older breeders were frequently not significant, estimates of natality for squirrels on our study areas, based only on yearling and older age categories (common in earlier studies), would not be greatly in error.

Introduction

Although natality in Belding's ground squirrels was estimated by several investigators (Grinnel and Dixon 1919, Bailey 1936, Howell 1938, McKeever 1964, Turner 1972, Sauer 1976), none classified ages of maternal females more precisely than to yearling and older categories. However, a relationship between maternal age and litter size was reported among several sciurid rodents (Slade and Balph 1974, Nixon and McClain 1975) and other mammals (Nalbandov 1976). Morton and Gallup (1975) reported that female *S. beldingi* 2 or more years old produced significantly more offspring than yearling females, but they did not separate the older squirrels into year classes. Because Sherman (1977) reported wild adult *S. beldingi* females in 2- to 8-year age classes, we believed that investigation of age-specific natality in a population of the species was warranted.

In earlier studies, division of the adult cohort into year classes seemingly was possible only by repeatedly livetrapping, over a period of years, individuals marked as juveniles (Morton and Parmer 1975, Morton and Gallup 1975). Klevezal' and Kleinenberg (1967) reported that lines in periosteal bone that stained more darkly than surrounding bone was formed annually in numerous, but not all, species of mammals; they referred to these lines as "adhesion lines." Millar and Zwickel (1972), Sullins *et al.* (1976), and Frylestam and von Schantz (1977) found adhesion lines useful in estimating ages of several lagomorphs; Livezey and Verts (1979) found a relationship between numbers of adhesion lines and ages determined by other criteria in geo-

[1]Present address: Mobil Coal Producing, Inc., P.O. Box 17772, Denver, Colorado 80217.

myids. To our knowledge, determination of age by counts of densely stained lines in bones of sciurid rodents in the western hemisphere was not attempted previously. If applicable, the technique would permit more precise estimates of natality in *S. beldingi*, a species of considerable economic importance (Sullins and Verts 1978).

Methods

During April-June 1975 and April-May 1976, 105 and 168 female Belding's ground squirrels were collected on the Oregon State University Harris Ranch (elevation = 1700 m) approximately 63 km southwest of John Day, Grant County, Oregon, respectively. In addition, 158 and 153 female squirrels were obtained from hunters who participated in an annual ground squirrel shoot on the adjacent Izee Ranch on 30 May 1975 and 1976, respectively.

The uterus of each squirrel was excised and examined for developing embryos and pigmented sites of implantation; viable and resorbing embryos were recorded separately. Mandibles were removed, defleshed, and air dried. In the laboratory, mandibles were decalcified in 5 percent nitric acid for 12 hours, or until flexible, and rinsed for 12 hours in running water. A segment from each mandible anterior to the molariform row was removed and cross-sectioned at 20-25 μ on a freezing microtome. Several sections from each mandible were mounted on slides with Mayer's albumen, stained with Papanicoloau (Harris) hematoxylin, and examined under a microscope for darkly stained lines. Numbers of darkly stained lines were recorded.

To determine if numbers of darkly stained lines were related to age, mandibles from 49 Belding's ground squirrels livetrapped, classified as young-of-the-year or older, marked, and released on the Harris Ranch in 1975 were collected in 1976. In addition, mandibles from 23 squirrels judged young-of-the-year on the basis of size and weight (Turner 1972) were collected in 1976. Mandibles were prepared and examined as described earlier; we expected those judged young-of-the-year to have no darkly stained lines, those marked as young-of-the-year and examined as yearlings to have one stained line, and those marked as older than young-of-the-year in 1975 to have two or more lines.

Student's t test or analysis of variance was used to ascertain the probability that numbers of embryos or implantation sites per female between age classes were significantly different depending on whether two or more than two age cohorts of females occurred in samples. In instances that analysis of variance indicated $P < 0.05$, Fisher's protected least significant difference test was used to ascertain which mean rates were significantly different.

Results and Discussion

Among the 23 young-of-the-year ground squirrels collected in 1976, all possessed mandibles without stained lines; among those marked in 1975 and collected in 1976, 20 (95.2 percent) of 21 yearlings had one line and 27 (96.4 percent) of 28 older squirrels had two or more lines. Apparently, one line was formed each year in *S. beldingi*; no squirrel exhibited evidence of resorbing adhesion lines.

Absence of stained lines in mandibles of 18 adult ground squirrels collected on the Harris Ranch in 1975 and 1976 (Table 1) seemed inconsistent with this conclu-

TABLE 1. Numbers of adult female Belding's ground squirrels with 0, 1, 2, and 3 adhesion lines in their mandibles in each collection, 17 April-20 June 1975 and 7 April-31 May 1976, Harris Ranch, Grant County, Oregon.

Date of collection		Squirrels examined	Number of adhesion lines			
Year	Day and Month	(N)	0	1	2	3
1975	17 April	23	8	10	5	
	21 April	21	2	11	8	1
	3 May	19	1	10	7	1
	10 May	16		11	5	
	20 June	25		17	8	
1976	7 April	24	6	6	12	
	14 April	24	1	12	10	1
	26 April	19		14	3	2
	2 May	27		11	14	2
	11 May	28		15	8	5
	18 May	21		10	9	2
	31 May	25		8	15	2

sion. These adults were collected before juveniles emerged from natal dens; hence, they were known to be at least 1 year old. Because similar discrepancies were not noticed among collections of squirrels made later in the season during both years (Table 1), we suggest that deposition of bone tissue sufficient to distinguish darkly stained lines from the stained outer surfaces of the mandibles had not occurred in these squirrels, a supposition consistent with those of Klevezal' and Kleinenberg (1967). Seasonal differences in proportions of female squirrels without discernible stained lines in their mandibles (Table 1) possibly were related to differences in phenology between 1975 and 1976 (Costain 1978). Because 17 (94.4 percent) of 18 squirrels without stained lines were nulliparous whereas only 17 (6.7 percent) of 255 with lines were nulliparous, we suspect that females without lines were collected shortly after they emerged from dormancy and before their first estrus, or possibly some were late-born young of the previous year that did not breed as yearlings.

We believe that the strong relationship between numbers of darkly stained lines in mandibles of ground squirrels and numbers expected on the basis of their known ages or known minimum ages, and evidence that individuals whose darkly stained lines were not discernible were assignable to the 1-year adult cohort, is justification for separating samples of Beldin's ground squirrels into age classes by the periosteal zonation technique.

TABLE 2. Numbers of implantation sides ($\bar{X}$±S.E.) for parous[1] Belding's ground squirrels with 0, 1, 2, and 3 adhesion lines in periosteal zones of their mandibles, Izee Ranch, Grant County, Oregon, 30 May 1975 and 1976.

	1975		1976	
Adhesion lines (N)	Females examined (N)	Implantation sites ($\bar{X}$±S.E.)[2]	Females examined (N)	Implantation sites ($\bar{X}$±S.E.)[2]
0	0		0	
1	97	6.0±0.2	82	6.4±0.2
2	51	6.6±0.2[a]	66	7.1±0.2
3	3	8.0[a]	3	10.3

[1]In 1975, seven females with one adhesion line were nulliparous; in 1976, two with one adhesion line were nulliparous.

[2]Means within a collection and in the same column followed by the same letter were not significantly different ($P > 0.05$).

TABLE 3. Reproductive performance of female Belding's ground squirrels with 0, 1, 2, and 3 adhesion lines in periosteal zones of their mandibles, Harris Ranch, Grant County, Oregon, 1975-76.

Category	Number of adhesion lines (1975)				Number of adhesion lines (1976)			
	0	1	2	3	0	1	2	3
Adult females examined (N)	11	59	33	2	7	76	71	14
Females nulliparous (N)	11	3	4		6	7	3	
Females pregnant (N)		31	18	2	1	29	26	3
Postpartum females (N)		16	11			40	42	11
Viable embryos/pregnant female (X±S.E.)[1]		5.1±0.2a	5.8±0.4a	6.5	5	4.5±0.2b	5.9±0.2	3.7b
Females with resorbing embryos (N)		4	3			6	5	
Resorbing embryos/pregnant female (X)		0.1	0.2			0.3	0.3	
Implantation sites/postpartum female (X±S.E.)[1]		4.4±0.3	5.5±0.3			5.1±0.2	5.9±0.2c	6.3±0.3c

[1]Means within a collection and in the same row followed by the same letter were not significantly different ($P > 0.05$).

Except for third-cohort pregnant females on the Harris Ranch in 1976, mean litter sizes based on counts of viable embryos and implantation sites increased with maternal age (Tables 2 and 3); analysis of variance indicated differences within collections were significant ($P < 0.05$), except those for pregnant females obtained on the Harris Ranch in 1975 (Table 3). Seemingly, differences in mean numbers of embryos or implantation sites between first- and second-cohort breeders were responsible for significant differences within collections; in only two of five instances were mean numbers of embryos or implantation sites significantly different between second- and third-cohort breeders (Tables 2 and 3).

Because numbers of Belding's ground squirrels in cohorts with more than two adhesion lines were low, and because differences in litter sizes between second-cohort and older breeders frequently were not significant, we believe that estimates of natality for squirrels on our study areas based on only two age categories (yearlings and older squirrels) would not be greatly in error.

Although Sherman (1977) did not report the proportion of the 1135 *S. beldingi* that he marked that were in each sex and age class, we suspect that the number of females older than 3 years was relatively small. However, the relative infrequency of ground squirrels with three adhesion lines and the absence of squirrels with four or more lines (Tables 2 and 3) suggested that the dynamics of populations of Belding's ground squirrels on our study areas were somewhat different from those in California that Sherman (1977) studied. We speculate that reduction of numbers of ground squirrels by routine control programs (Sullins and Verts 1978) or the annual ground squirrel shoot truncated age distributions of squirrels on our study areas.

Acknowledgments

We thank R. A. Anthony and J. A. Crawford for critiques of the manuscript. This is Technical Paper No. 5522, Oregon Agricultural Experiment Station.

Literature Cited

Bailey, V. 1936. The mammals and life zones of Oregon. N. Amer. Fauna 55: 1-416.

Costain, D. B. 1978. Dynamics of a Population of Belding's Ground Squirrels in Oregon. Oregon State Univ., Corvallis, M.S. thesis.

Frylestam, B., and T. von Schantz. 1977. Age determination of European hares based on periosteal growth lines. Mammal Rev. 7:151-154.

Grinnel, J., and J. Dixon. 1919. Natural history of the ground squirrels of California. Monthly Bull. State Comm. Hort. 7:597-708.

Howell, A. H. 1938. Revision of the North American ground squirrels. N. Amer. Fauna 56:1-256.

Klevezal', G. A., and S. E. Kleinenberg. 1967. Age determination of mammals from annual layers in teeth and bones. Acad. Sci. USSR, Severtsov Inst. Anim. Morphol. Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, 1969.

Livezey, B. C., and B. J. Verts. 1979. Estimates of age and age structure in Mazama pocket gophers, *Thomomys mazama*. Murrelet 60:38-41.

McKeever, S. 1964. Reproduction in *Citellus beldingi* and *C. lateralis* in northeastern California. Symp. Zool. Soc. London 15:365-385.

Millar, J. S., and F. C. Zwickel. 1972. Determination of age, age structure, and mortality of the pika, *Ochotona princeps* (Richardson). Can. J. Zool. 50:229-232.

Morton, M. L., and J. S. Gallup. 1975. Reproductive cycle of the Belding ground squirrel (*Spermophilus beldingi beldingi*): seasonal and age differences. Great Basin Nat. 35:427-433.

———, and R. J. Parmer 1975. Body size, organ size, and sex ratios in adult and yearling Belding ground squirrels. Great Basin Nat. 33:305-309.

Nalbandov, A. V. 1976. Reproductive Physiology of Mammals and Birds: the Comparative Physiology of Domestic and Laboratory Animals and Man. 3rd ed. W. H. Freeman and Company, San Francisco.

Nixon, C. M., and M. W. McClain. 1975. Breeding seasons and fecundity of female gray squirrels in Ohio. J. Wildl. Manage. 39:426-438.
Sauer, W. C. 1976. Control of the Oregon ground squirrel (*Spermophilus beldingi oregonus*). Proc. Vert. Pest Conf. 7:99-109.
Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. Science 197:1246-1253.
Slade, N. A., and D. F. Balph. 1974. Population ecology of Unita ground squirrels. Ecology 55: 989-1003.
Sullins, G. L., D. O. McKay, and B. J. Verts. 1976. Estimating ages of cottontails by periosteal zonations. Northw. Sci. 50:17-22.
———, and B. J. Verts. 1978. Baits and baiting techniques for control of Belding's ground squirrels. J. Wildl. Manage. 42:890-896.
Turner, L. W. 1972. Autecology of the Belding Ground Squirrel in Oregon. Univ. of Arizona, Tucson, Ph.D. thesis.

Received August 15, 1980
Accepted for publication September 2, 1980

Graham W. Smith[1]
Department of Zoology
Washington State University
Pullman, Washington 99164

Habitat Use by Porcupines in a Ponderosa Pine/ Douglas-fir Forest in Northeastern Oregon

Abstract

Habitat utilization by porcupines (*Erethizon dorsatum*) was studied primarily by capture-recapture and radiotelemetry methods. Porcupines spent their daylight hours in large trees within ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) stands. Such stands offered protection from effects of weather and offered an abundance of young trees on which to feed. Porcupines fed nocturnally during spring and summer within meadows where grasses and forbs were abundant.

Introduction

Little information on habitat use by porcupines has been reported for ponderosa pine/ Douglas-fir forests (Taylor 1935, Hoffer 1967, Randall 1971) and nowhere, to my knowledge, has a statistical treatment of habitat use been reported. Such information should be valuable to forest managers because porcupines frequently cause extensive silvicultural damage to timber (Taylor 1935, Lawrence 1957). The porcupine is distributed throughout most of North America, occurring from the Atlantic to the Pacific Oceans (Hall and Kelson 1959). Habitat preferences vary with geographical location and differences in vegetation types. This report discusses porcupine habitat use in a ponderosa pine and Douglas fir forest in northeastern Oregon.

Study Area

The study area was within the Heppner Ranger District of the Umatilla National Forest, located 60 km south of Heppner, Oregon. The Forest, at the southwestern edge of the Blue Mountains, is a narrow band of rolling, forested hills cut by drainages. Elevations vary from 1200 to 1900 m.

Seven plant communities were identified using Hall's (1973) classification.

1. *Bluegrass scabland.* This community had sparse Sandberg bluegrass (*Poa sandbergii*) as the primary dominant.

2. *Bunchgrass on deep soils, gentle slopes.* Mountain meadows dominated by bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and Sandberg bluegrass.

3. *Juniper-bunchgrass.* This community had widely spaced juniper (*Juniperus occidentalis*) and ponderosa pine trees with a mixed grass ground cover.

4. *Juniper-low sagebrush.* Juniper trees were few and widely scattered. Low sagebrush (*Artemisia arbuscula*) and bitterbrush (*Purshia tridentata*) were the dominant species.

[1]Present address: Department of Fisheries and Wildlife, Utah State University, Logan, Utah 84322.

5. *Ponderosa pine/Douglas-fir/elk sedge.* Characterized by ponderosa pine with some Douglas fir and juniper and a ground cover dominated by cheatgrass (*Bromus tectorum*), rattlesnake grass (*Bromus brizaeformis*), and elk sedge (*Carex geyeri*), this community had widely scattered trees.

6. *Mixed conifer-pinegrass, residual soil.* This community was present as two distinct subunits. One subunit consisted of nearly pure stands of ponderosa pine. Understory vegetation was a mixture of grasses and herbaceous plants. The other subunit consisted of stands on hilltops where Douglas-fir was the dominant tree species. Grasses were reduced and there was a greater abundance of herbaceous plants.

7. *White fir-twinflower-forb.* White fir (*Abies concolor*) and Douglas-fir occurred in dense stands with seedlings occupying all openings on the forest floor. Western larch (*Larix occidentalis*) occurred in small numbers. Along the creek beds, Engelman spruce (*Picea engelmannii*) replaced Douglas-fir.

Methods

Field work was conducted from June 1973 through August 1974. A total of 168 porcupines were captured and tagged. Of these, 116 were taken from June through September by driving a 7.6 km route at night and capturing individuals seen in the headlights. An additional 52 animals were captured from trees or dens during the day from October through May, within a 259 ha (1 sq. mi.) intensive-study plot. Nine porcupines were tagged with radio transmitters as described by Marshall *et al.* (1962) and were radio-tracked from February through August 1974, for a total of 495 animal-days. All radio-equipped animals ranged within the intensive-study plot and were observed only during daylight hours. Vegetation type was recorded for all porcupine capture and observation locations.

Daytime locations of porcupines within the intensive-study plot, and summer nocturnal and crespuscular locations were used to calculate porcupine habitat preferences using the procedure described by Neu *et al.* (1974). A 'family' of confidence intervals was constructed using the Bonferroni normal statistics, and a standard significance level of $P = 0.10$ was used to study preference for or avoidance of individual habitat types. Inherent in the use of the procedure is the assumption that individual porcupines had the opportunity to select any of the plant communities present. This assumption appears valid, although not all plant communities were evenly distributed throughout the study area.

Results and Discussion

A goodness-of-fit comparison ($\chi^2 = 40.59$, d.f. $= 5$, $P < 0.005$) indicates porcupine use of plant communities differed significantly from the occurrence of the plant communities within the intensive-study plot (Table 1).

There was a significant preference for the mixed conifer-pinegrass, residual soil plant community. This was true both for the ponderosa pine dominant and the Douglas fir dominant subunits. In addition, a significant avoidance of the ponderosa pine/Douglas-fir/elk sedge community occurred. Sample sizes for the two juniper types were insufficient to accurately predict porcupine usage.

Daily resting locations of porcupines in northeastern Oregon were strongly influ-

TABLE 1. Occurrence of daytime resting locations of porcupines within plant communities in northeastern Oregon.

Plant community	Number of porcupines observed	Expected number of porcupines	Proportion observed in each community P_i	Total hectares	Proportion of total hectares	Confidence interval on proportion of occurrence (90% confidence coefficient)
Juniper-bunchgrass	4	9	0.016	8.98	0.038	$0.000 < P_i < 0.035$*
Juniper-low sagebrush	3	9	0.012	8.66	0.037	$0.000 < P_i < 0.037$
Ponderosa pine/Douglas-fir/ elk sedge	44	68	0.177	63.98	0.271	$0.119 < P_i < 0.235$*
Mixed conifer-pinegrass, residual soil (Ponderosa pine dominant)	52	27	0.209	25.66	0.019	$0.147 < P_i < 0.271$*
(Douglas-fir dominant)	63	48	0.253	45.45	0.193	$0.197 < P_i < 0.319$*
White fir-twinflower-forb	83	88	0.333	83.13	0.352	$0.262 < P_i < 0.402$

*Significant $P < 0.01$.

enced by porcupine food habits (Smith 1979). Porcupines fed on herbaceous ground vegetation from April through August. During this period they rested in trees or dens during the day and fed on ground vegetation at dusk. Movements from one day's resting location to the next were extensive as porcupines fed. By the end of August ground vegetation had dried out and porcupines fed almost exclusively in trees on tree innerbark (phloem) and needles. With the arrival of winter weather, porcupine movements decreased substantially compared with those of spring and summer. Movements were short trips from one tree to the next, or from dens or trees located in the immediate area of the den (Smith 1979). This seasonal variation in feeding is similar to that observed for porcupines throughout their geographic range (Dodge 1967). Seasonal use of ponderosa pine vegetation types in northeastern Oregon was similar to that observed for ponderosa pine types in Arizona (Taylor 1935) and California (Hoffer 1967).

Daily resting locations of porcupines were a result of porcupine food and tree density preferences (Smith 1975). The mixed conifer community had a much higher tree density than the ponderosa pine/Douglas-fir/elk sedge community. This high density offered an abundance of young trees, those most commonly fed upon, and offered protection from climatic factors such as wind and snow (Smith 1979). The ponderosa pine/Douglas-fir/elk sedge community consisted mainly of widely scattered trees of small diameter and did not offer the food and protection of the mixed conifer community.

Porcupines preferred to rest in large size trees. Ponderosa pine was preferred, with greatest use (33 percent of total) in the 31-55 cm diameter breast height (dbh) category. These trees were 90 to 180 years old and were the most common large trees in the intensive-study plot. Trees greater than 56 cm dbh were one-sixth as common and did not occur in dense stands.

Douglas-fir, 31 to 56+ cm dbh, received high use (28.2 percent of total) as rest trees. These trees occurred in the mixed conifer-pinegrass community and in the white

fir-twinflower-forb community. Mistletoe-infested Douglas-fir were often used during inclement weather when porcupines would rest in 'witches brooms' that offered protection from snow and wind (Smith 1979). Similar behavior was noted by Hoffer (1967) in a pine-juniper forest in northern California.

Porcupines used the same trees repeatedly. Porcupines rested in a tree they had previously used 67 times. Porcupines were observed to rest in trees previously used by different porcupines on ten occasions. Similar use of certain trees by several animals was noted by Randall (1971).

Spring and summer crespuscular and nocturnal locations of porcupines within plant communities along the 7.6 km route indicated that porcupine occurrence within the plant communities differed significantly ($\chi^2 = 13.21$, d.f. $= 3$, $P < 0.005$) from the proportions of the plant communities along the route (Table 2). The preference for the bunchgrass community and avoidance of the ponderosa pine dominant subunit of the mixed conifer community was related to porcupine nocturnal feeding behavior: porcupines rested in the mixed conifer community during the day and left this vegetation type at dusk to feed on ground vegetation. The bunchgrass community occurred in meadows and contained a greater abundance of the most commonly selected foods than any other community along the route.

TABLE 2. Occurrence of nocturnally moving and feeding porcupines within plant communities in northeastern Oregon.

Plant community	Number of porcupines observed	Expected numbr of porcupines	Proportion observed in each community P_i	Proportion of total route	Confidence interval on proportion of occurrence (90% confidence coefficient)
Bunchgrass on deep soils, gentle slopes	48	28	0.265	0.152	$0.192 < P_i < 0.338$*
Ponderosa pine/Douglas-fir/ elk sedge	49	41	0.265	0.221	$0.192 < P_i < 0.337$
Mixed conifer-pinegrass residual soil					
(Ponderosa pine dominant)	77	102	0.417	0.555	$0.336 < P_i < 0.498$*
(Douglas-fir dominant)	10	13	0.053	0.072	$0.016 < P_i < 0.090$

*Significant $P < 0.10$.

Randall (1971) also noted that nocturnal use of meadow types by porcupines was high in spring and summer. Most of Randall's nocturnal porcupine captures occurred within meadows. Marshall *et al.* (1962) believed one of their radio-equipped porcupines fed exclusively within a spruce bog at night. The spruce bog probably offered the widest variety of succulent ground vegetation. Hoffer (1967) reported that porcupines in northern California made extensive use of alfalfa fields. Although not a natural situation, the use of alfalfa is again indicative of the porcupines' preference for lush herbaceous vegetation. This preference appears to be a major determinant of habitat use by porcupines in the spring and summer. In comparison, the availability of young trees as a source of inner-bark and needle food, in or near relatively dense stands of large trees, seems to restrict porcupine movements in the fall after ground vegetation dries out and later in the year when the larger trees provide a refuge from winter weather.

Acknowledgments

I thank R. E. Johnson and R. J. Jonas for their counsel and support during this project, and H. Black, S. S. Devlin, D. W. Martin, and C. E. Rouse for their assistance in the field. I also thank J. R. Hargis for his constructive comments on an earlier draft of the manuscript. This project was funded in part by the U.S. Forest Service and by a grant-in-aid of research from the Society of the Sigma Xi; it was submitted in partial fulfillment for the M.S. degree in Wildlife Biology at Washington State University.

Literature Cited

Dodge, W. E. 1967. The Biology and Life History of the Porcupine in Western Massachusetts. Univ. Massachusetts, Amherst. Ph.D. thesis.

Hall, E. R., and K. R. Kelson. 1959. The Mammals of North America. Ronald Press Co., New York.

Hall, F. C. 1973. Plant Communities of the Blue Mountains in Eastern Oregon and Washington. U.S. For. Serv., Pacific Northwest Region. Pub. No. R6-82000-1.

Hoffer, M. C. 1967. Radio-telemetry: a key tool in porcupine control-methods research. Trans. California-Nevada Sect. Wildlife Soc.

Lawrence, W. H. 1957. Porcupine Control: A Problem Analysis. Weyerhaeuser Timber Co. Forest Res. Notes.

Marshall, W. M., G. W. Guillion, and R. G. Schwab. 1962. Early summer activities of porcupines as determined by radio-positioning techniques. J. Wildl. Manage. 26:75-79.

Neu, C. W., D. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-542.

Randall, R. C. 1971. The Distribution, Movement Patterns, and Population Structure of the Porcupine (*Erethizon dorsatum*) in Little Valley, Nevada. Univ. Nevada, Reno, M. S. thesis.

Smith, G. W. 1975. An Ecological Study of the Porcupine (*Erethizon dorsatum*) in the Umatilla National Forest, Northeastern Oregon. Washington State Univ., M.S. thesis.

———. 1979. Movements and home range of the porcupine in Northeastern Oregon. Northw. Sci. 53:277-282.

Taylor, W. P. 1935. Ecology and life history of the porcupine (*Erethizon epixanthum*) as related to the forests of Arizona and the South-Western United States. Univ. Ariz. Bull. 3:1-177.

Received July 21, 1980
Accepted for publication October 28, 1980

Robert E. Batie[1]

Department of Zoology
Oregon State University
Corvallis, Oregon 97331

Population Structure of the Crab Hemigrapsus oregonensis (Brachyura, Grapsidae) in Yaquina Bay Estuary, Oregon. II. Vertical Distribution, Biomass, and Production

Abstract

The vertical distribution of the intertidal shore crab *Hemigrapsus oregonensis* at Coquille Point in the Yaquina Bay Estuary, Oregon, was studied. Population density increased from the 1-2 ft vertical interval (7.89 crabs/m^2) to the 3-4 ft vertical interval (20.09 crabs/m^2). A model for estimating each crab's dry weight is given ($r = 0.98$). Biomass increased as tidal height increased up to the 3-4 ft interval. Maximum biomass was 10.182 g/m^2. The average monthly production rate was −1.23 g/m^2 per month, a loss of about 2.3 average (carapace width 1.5 cm) crabs/m^2 per month from the population.

Introduction

Many factors have been proposed to explain the vertical distribution of intertidal organisms (Johnson and York 1915, Colman 1933, Doty 1946, Hutchins 1947, Stephenson and Stephenson 1949, Connell 1961, Ricketts *et al.* 1968). *Hemigrapsus oregonensis*, a small intertidal shore crab found from Alaska to the Gulf of California (Schmidt 1921, Hart 1968), is vertically stratified within its range. This study was conducted to characterize the vertical distribution of the *H. oregonensis* population at Coquille Point in the Yaquina Bay Estuary, Oregon.

Methods

The study area at Coquille Point (44° 37′ N. Lat.; 124° 04′ W. Long.) in the Yaquina Bay Estuary was marked out in a grid from the 0 ft tidal level to the 5 ft tidal level at 1 ft vertical intervals. Five adjacent subplots were established at each tidal height interval. Each of the 25 subplots had an area of about 3 m^2. Each month during the spring tidal cycle, one subplot at each tidal height was randomly selected and sampled using a complete population census. All crabs were hand-captured, sexed, measured, and returned to the same subplot from which they were captured. Measurements of carapace width, taken from the second lateral carapace tooth to the second lateral carapace tooth, were made with an Almkvist excaliper and reported to the nearest one hundredth of a centimeter. A dry weight conversion equation was established from specimens killed and held in formalin for not longer than 48 hours. The crabs were sexed, measured, and dried in an oven at 85° C to constant weight (usually within 48 h). The dry weight value of each crab was then regressed on several other variables using a step-wise multiple regression technique (Snedecor and Cochran 1961). Bio-

[1]Present address: Department of Biology, Radford University, Radford, Virginia 24142.

mass estimates were made for each tidal height from measurements of carapace width (variable of best fit) of each crab and from counts of numbers of crabs in each tidal height interval. Monthly biomass values (g/m^2) were determined for each tidal height. Production estimates were determined from the net gain or loss in biomass at each tidal level from one month to the next. Production estimates are reported as biomass fluctuation per unit time (Chapman 1968) and are not meant to imply the inclusion of relative growth rate data.

Results and Discussion

The number of crabs captured during the study period varied with tidal height (Fig. 1). The mean number of crabs captured per month at each tidal height was compared with the mean numbers at all other tidal heights. Monthly mean numbers of crabs were significantly different ($p < .05$) from monthly mean numbers of crabs from other tidal heights, except for the 3-4 ft interval when compared with the 4-5 ft interval.

A population size class frequency distribution (Fig. 2) indicated that the majority of the population was between 1.20 and 1.95 cm in carapace width with a mean of about 1.50 cm. Since it was observed that a crab increased in carapace width by 0.26 cm per molt (from 1.11 cm to 1.37 cm), and since these crabs may molt several times per year, the peak in the distribution may represent the first year class. Since there

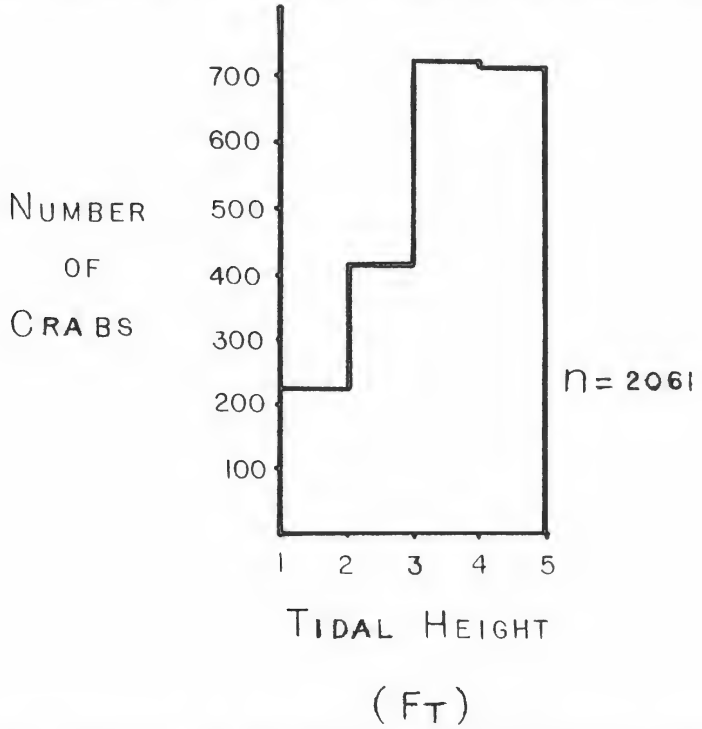


Figure 1. Histogram of number of crabs collected at each tidal height interval at Coquille Point from April, 1972 through May, 1973.

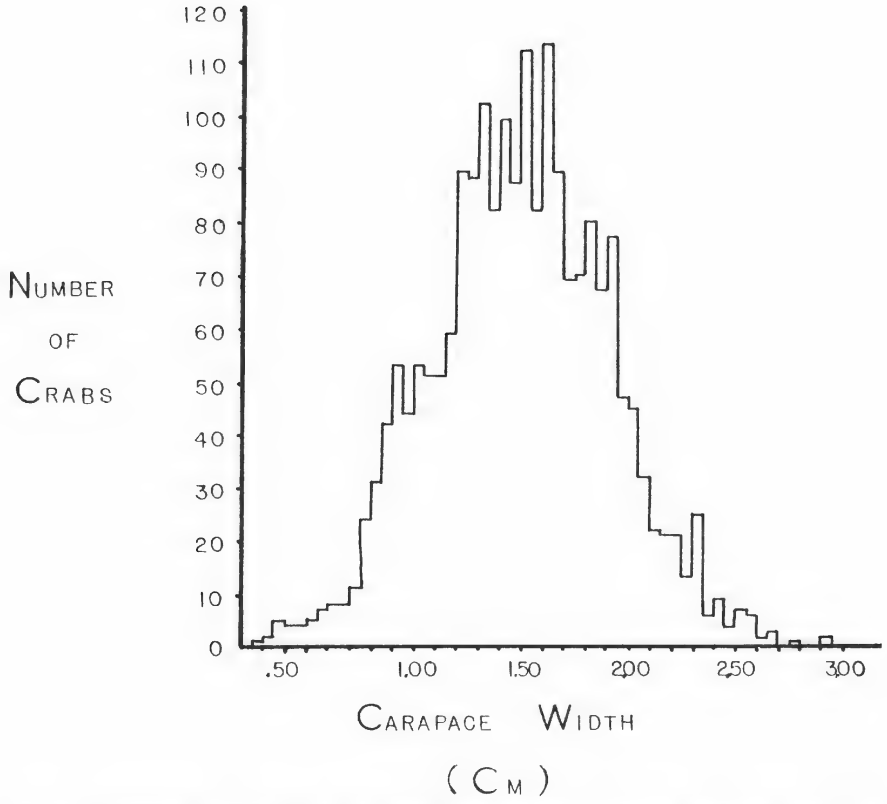


Figure 2. Histogram showing number of crabs in each carapace width size class from April, 1972 through May, 1973. Size class interval is 0.05 cm.

was a rapid decline at the larger carapace widths, a large population turnover each year was indicated. One would not expect, then, few crabs of smaller carapace width. Large numbers of smaller crabs (0.20 to 1.00 cm) could be expected to account for the large central (1.00 to 2.00 cm) portion of the population. Possible explanations of so few smaller crabs and so many intermediate sized crabs might be 1) that the intermediate sized crabs represented many years of recruitment from the smaller sized crabs (implies greatly reduced growth rates), 2) that sampling efficiency on smaller sized crabs was not as high as on large sized crabs, or 3) that immigration of intermediate sized crabs occurred. The problem was not fully resolved. However, due to the large size gain per molt and the frequency of molts, it is doubtful that the intermediate sized crab peak (1.00 to 2.00 cm) was the result of many years of recruitment. Sampling efficiency may have accounted for some bias in the smaller sized crabs (0.20 to 0.50 cm), but sampling efficiency above the 0.50 cm size class was not thought to be different from any other size class since crabs of this size are readily visible. The last hypothesis, settling of the young crabs outside the study area coupled with later immigration into it, can not be discounted. A high population mobility has been observed. It appears that immigration of smaller crabs into the study area bal-

anced the loss, due to emigration and high mortality rates, of larger crabs in the study area. The settling site of these young crabs was not investigated. The study site, however, was surrounded on either side by extensive mudflats and subtidally by mudflats and *Zostera* beds.

In order to realistically estimate biomass without depleting the study population, an easily obtained field measurement of some parameter related to biomass was needed. This parameter could later be converted to a biomass figure. To obtain such a parameter, the log of crab carapace width (in centimeters) was regressed on the log of crab dry weight (in grams) (Fig. 3). A dummy variable for crab sex was included in the model to test for differences between the dry weight of male and female crabs of the same carapace width. The model is:

log (dry weight of male in grams) $= -2.007 + 3.065$ X log (carapace width in cm)
log (dry weight of female in grams) $= -2.028 + 3.065$ X log (carapace width in cm)

Since there is such high correlation between these two parameters ($r = 0.98171$), this model has excellent predictive powers for dry weight estimations given a crab's sex and carapace width.

The average dry weight per crab (Fig. 4) showed a monthly average which was fairly constant throughout spring and summer but decreased dramatically in late fall and early winter. The large increase in weight per crab from October to November suggested that few small crabs were recruited to the population at this time and that existing crabs increased in weight. Since a lag of about 8 to 13 weeks is necessary for an egg brood to hatch, metamorphose, and be recruited into the adult population, low recruitment in November and December would be expected. Coupled with unfavorable settling conditions, few of these larvae may be recruited; hence, an increase in the average dry weight in the population would be expected. The large decrease in average dry weight per crab in January was a reflection of either increased larval settling success or a differential mortality rate on larger crabs, assuming no immigration or emigration. However, a large January recruitment was not realized (Batie 1982). A differential mortality rate on larger crabs was not demonstrated.

The mean average dry weight per crab decreased as tidal height increased, sug-

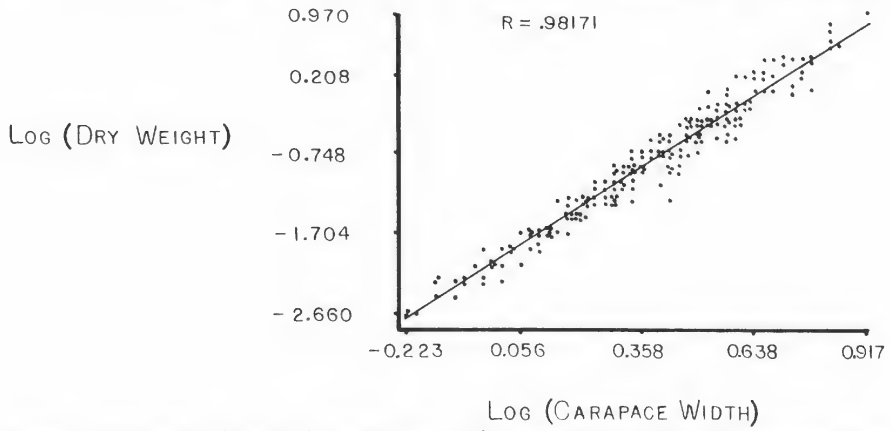


Figure 3. Relationship between dry weight (g) and carapace width (cm) in *Hemigrapsus oregonensis* from Coquille Point in the Yaquina Bay Estuary, Oregon.

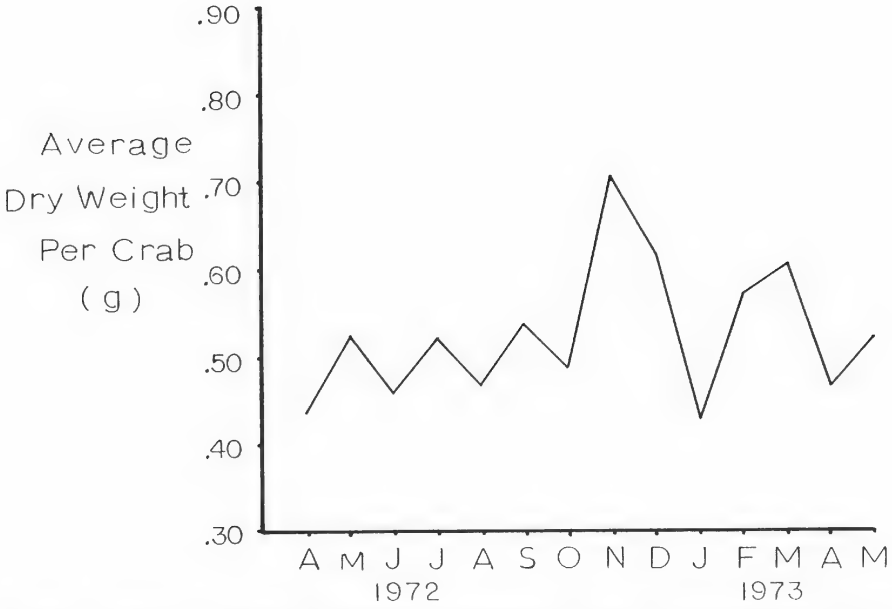


Figure 4. Average dry weight of *Hemigrapsus oregonensis* at Coquille Point from April, 1972 through May, 1973.

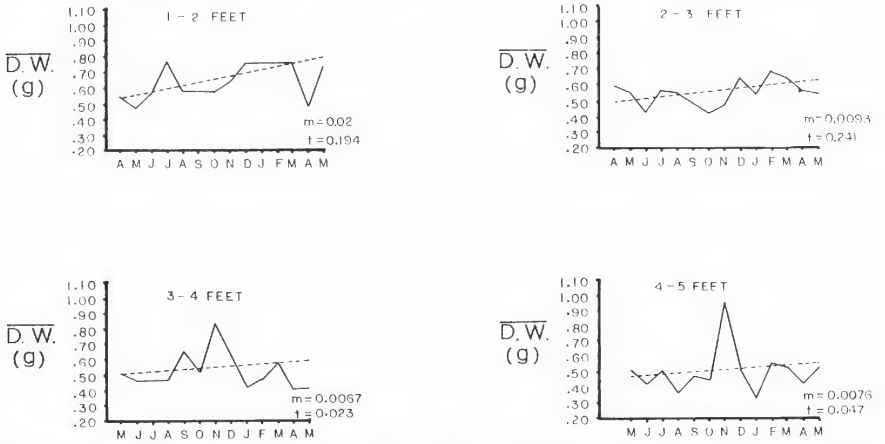


Figure 5. Average dry weight per crab from April, 1972 through May, 1973 at various tidal heights. Slope coefficient represented by m, t represents t-value for testing if slope coefficient is different from a zero value. Slope was not found to be different from zero in any of the cases ($p > .05$).

gesting a vertical segregation of crabs by size. When the average dry weight per crab was plotted for each month at each tidal height (Fig. 5), it appeared as though a general increase in average dry weight per crab occurred during the study. A regression line was fitted to the data and the slope coefficient was tested to determine if it was significantly different from zero. In each case, the slope coefficient could not be shown

to be significantly different from zero ($p > .05$); hence, the apparent average dry weight increase can not be statistically substantiated. Since the average dry weight per crab did not significantly increase during the year, this suggested that the population was stable.

It was of interest, however, to further investigate the apparent size segregation by tidal height. The crabs in the 1-2 ft tidal interval were significantly heavier ($p < .05$) than the crabs in levels 2-3, 3-4, or 4-5 ft. Crabs in levels 2-3, 3-4, and 4-5, however, were not significantly different from each other. This finding implied that the smaller crabs were limited to the upper regions of the study area and invaded the lower areas only as their size increased. Further, this implied that 1) settlement behavior of the metamorphosing larvae led to a selection of the upper habitat areas, 2) some biological or physio-chemical barriers drove the small crabs from the lower areas, or 3) greater mortality rates existed in the lower regions for the small crabs.

In addition to the study area being vertically stratified by number and size of crabs, the area also showed a definite biomass segregation by tidal height. The average monthly biomass in g/m^2 at the various tidal heights (Fig. 6) showed an increase in biomass as tidal height increased up to the 3-4 ft level and then decreased slightly at the 4-5 ft level. The biomass average ranged from 1.14 g/m^2 to 10.18 g/m^2. The biomass at each tidal level during the year showed less variation in the lower levels than in the upper levels. There was no significant change in biomass figures for any tidal height during the study period ($p > .05$). Constant biomass at the various tidal heights indicated a stable population during the study.

The mean monthly biomass at the 1-2 ft interval was significantly different ($p < .01$) from the biomass values at all other tidal levels. The mean monthly biomass values at the 3-4 ft and the 4-5 ft tidal levels, however, could not be shown to be significantly different ($p > .05$).

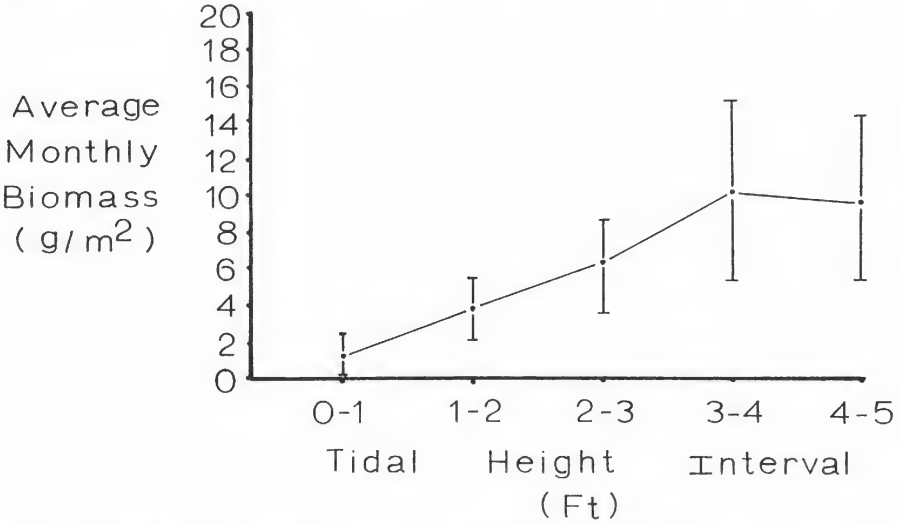


Figure 6. Average monthly biomass in g/m^2 for *Hemigrapsus oregonensis* at Coquille Point from April, 1972 through May, 1973. Vertical bars indicate standard error about means, which are connected by solid lines.

The maximum biomass values for the bay population of crabs, about 10 g/m^2, was higher than that reported for carnivorous reef crabs from Eniwetok atoll (5.5 g/m^2) (Odum and Odum 1955). Since *Hemigrapsus* is predominantly a herbivore (Knudsen 1964), comparisons between trophic levels may not be directly meaningful. Odum and Odum (1955) have, however, estimated that the conversion efficiency ratio between carnivores and herbivores is 8.3 percent. About 63 g/m^2 of herbivores would be required to support the 5.5 g/m^2 of carnivorous crabs. This 63 g/m^2 is about six times the biomass value found for the herbivorous *Hemigrapsus* and suggests that the Yaquina Bay crab standing crop is considerably less than the equivalent standing crop of this reef community. Additional biomass studies in Puerto Rico (Golley *et al.* 1962) have indicated that crabs, mostly fiddler crabs (*Uca*), reached biomass estimates of up to 5.1 g/m^2 in mangrove swamps. Teal (1962), however, has reported *Uca* biomass estimates of nearly 115 g/m^2 in Georgian salt marshes. The Yaquina Bay biomass values for *Hemigrapsus oregonensis* are nearer the lower limits of the biomass range reported for other intertidal crabs.

The average monthly production rate (g/m^2 per month) at each tidal height is plotted in Figure 7. The 0-1 ft level and the 1-2 ft level showed an average negative production rate of about –0.10 g/m^2 per month. The 2-3 ft level showed a greater negative production value, while the 3-4 ft level showed the greatest negative production. Average monthly production was highest in the 4-5 ft level. The negative productions in the lower regions suggested that the population was declining or that emigration was occurring from these regions. The net monthly production rate at the site was about –1.23 g/m^2 per month or about the equivalent of 2.3 average (carapace width = 1.5 cm) crabs lost from the population per month per m^2.

Although the biomass for each tidal height was significantly different from all other tidal heights, the mean production values for the various levels were near a zero

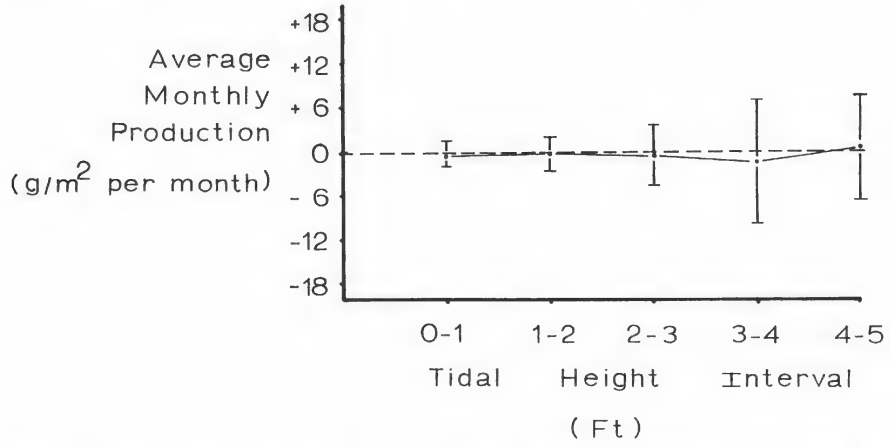


Figure 7. Average monthly production rate in g/m^2 per month for *Hemigrapsus oregonensis* at Coquille Point from April, 1972 through May, 1973. Dashed line represents zero production rate of stable population. Means are connected by solid line. Vertical bars indicate standard error about means. T-tests between means and between zero production rate were not significantly different ($p > .05$). Production, as used here, is synonymous with standing crop fluctuation per unit time and is not meant to imply the inclusion of relative growth rate data.

value. A zero value of biomass fluctuation per unit time would indicate a stable population. To determine if such a rate existed, a t-test between means for each tidal height interval was performed. It was found that the mean production rate for each tidal height was not significantly different ($p > .05$) from any other tidal height. From a comparison of the mean production rate of the 3-4 ft interval with the 4-5 ft interval (greatest range in production), it can be determined that no production rate is significantly different from a zero production rate ($p > .05$). Hence, an argument is presented that, with respect to production, the population was stable during the study period.

Summary and Conclusion

The *Hemigrapsus oregonensis* population at Coquille Point in the Yaquina Bay Estuary was not evenly distributed from the 1 ft to the 5 ft tidal level. The 1-2 ft interval had an average of 7.89 crabs/m^2, the 2-3 ft interval had 11.84 crabs/m^2, the 3-4 ft interval had 20.09 crabs/m^2, and the 4-5 ft interval had 19.73 crabs/m^2. A regression equation between carapace width and dry weight was established as a method of obtaining biomass and production estimates.

log (dry weight of male in grams) $=-2.007+3.065$ X log (carapace width in cm)

log (dry weight of female in grams) $=-2.028+3.065$ X log (carapace width in cm)

The mean monthly average dry weight per crab decreased as tidal height increased. The average dry weight per crab did not increase during the study. The average monthly biomass in g/m^2 increased significantly as tidal height increased up to the 3-4 ft interval. The mean monthly biomass value for the 1-2 ft interval was 3.807 g/m^2, the 2-3 ft interval 6.229 g/m^2, the 3-4 ft interval 10.182 g/m^2, and the 4-5 ft interval 9.782 g/m^2. Biomass values between the 3-4 and 4-5 ft intervals were not found to be significantly different. The average biomass value for all tidal heights was 8.47 g/m^2. The average monthly production was –1.23 g/m^2 per month, equivalent to a loss of about 2.3 average (carapace width 1.5 cm) crabs/m^2 per month from the population. This production rate, however, could not be shown to be statistically different from a zero production rate. No significant differences in production rates were found between any tidal heights.

Acknowledgments

I thank Dr. C. J. Bayne, Department of Zoology, Oregon State University, Corvallis, Oregon, for his help and guidance during this study. I also thank the Department of Zoology, Oregon State University, for providing the support which made this study possible. I extend special thanks to the Chesapeake Bay Center for Environmental Studies (Smithsonian Institution), Edgewater, Maryland, for providing space, guidance, and resources during the preparation of this manuscript.

Literature Cited

Batie, R. E. 1982. Population structure of the crab *Hemigrapsis oregonensis* (Brachyura, Grapsidae) in Yaquina Bay Estuary, Oregon. I. Reproductive cycle. Northw. Sci. 56:20-26.

Chapman, D. W. 1968. Production, pp. 182-196 *in* Methods for Assessment of Fish Production in Fresh Waters. W. E. Ricker (ed.). International Biological Programme Handbook 3. Blackwell Scientific Publications, Oxford.

Colman, J. 1933. The nature of the intertidal zonation of plants and animals. J. Mar. Biol. Ass.,

n.s. 18:435-476.
Doty, M. S. 1946. Critical tide factors that are correlated with vertical distribution of marine algae and other organisms along the Pacific coast. Ecology 27:315-328.
Golley, F., H. T. Odum, and R. F. Wilson. 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. Ecology 43:9-19.
Hart, J. F. L. 1968. Crab-like Anomura and Brachyura (Crustacea: Decapoda) from southeastern Alaska and Prince William Sound. Nat. Hist. Pap. Natn. Mus. Can. 38:1-6.
Hutchins, L. W. 1947. The bases for temperature zonation in geographic distribution. Ecol. Monogr. 17:325-335.
Johnson, D. S., and H. H. York. 1915. The relation of plants to tidal level. Carnegie Inst. Wash. Pub. 206.
Knudsen, J. W. 1964. Observations on the reproductive cycles and ecology of the common Brachyura and crab-like Anomura of Puget Sound, Washington. Pac. Sci. 18:3-33.
Odum, H. T., and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25:291-320.
Ricketts, E. F., and J. Calvin. 1968. Between Pacific Tides. Revised by J. W. Hedgpeth. 4th ed. Stanford Univ. Press. Stanford, Calif.
Schmidt, W. L. 1921. The marine decapod Crustacea of California. Univ. of Calif. Publ. Zool. 23.
Stephenson, T. A., and A. Stephenson. 1949. The universal features of zonation between tidemarks on rocky coasts. J. Ecol. 37:289-305.
Teal, J. M. 1962. Energy flow in a salt marsh ecosystem in Georgia. Ecology 43:614-624.
Snedecor, G. W., and W. G. Cochran. 1969. Statistical methods. Iowa State Univ. Press, Ames, Iowa.

Received April 15, 1980
Accepted for publication August 15, 1980

W. H. Rickard
and
R. H. Sauer
Pacific Northwest Laboratory
Ecological Sciences Department
Richland, Washington 99352

Primary Production and Canopy Cover in Bitterbrush-Cheatgrass Communities

Abstract

Aboveground grass and forb production averaged 126 $g \cdot m^{-2} \cdot yr^{-1}$ and ranged between 10 and 195 grams over a four year period 1975-1978. The low production year was 1977, a year of extreme drought. Production was not significantly different between unburned sites and burned sites five years post burning (1970). Canopy cover and species composition were similar on burned and unburned sites except for the shrubs, bitterbrush (*Purshia tridentata*) and sagebrush (*Artemisia tridentata*), which were killed by burning. There was no indication that shrubs were invading the burned areas as seedlings or vegetatively through sprouting. The implications of burning and mule deer (*Odocoileus hemionus*) management are briefly discussed.

Introduction

The bitterbrush-cheatgrass community is widely spread vegetal cover type at lower elevations on the Hanford Site, Benton Co., Washington (Fig. 1). It occupies sandy soils, and for the most part it lacks the perennial bunchgrass (*Stipa comata*) that characterizes herbaceous understory of bitterbrush (*Purshia tridentata*) stands in undisturbed condition (Daubenmire 1970). Instead, the understory is dominated by cheatgrass brome (*Bromus tectorum*). Perennial grasses are mostly represented by a sparse cover of Sandberg bluegrass (*Poa sandbergii*). Two large wildfires burned through parts of the bitterbrush community in 1963 and again in 1970. The 1970 fire reburned some of the same area as the earlier burn.

There are excellent published botanical descriptions of shrub steppe communities in pristine condition, but there is a paucity of data on primary productivity and botanical descriptions of shrub steppe communities in other than pristine condition (Daubenmire 1970). Primary production has been measured in stands representative of the *Artemisia tridentata/Agropyron spicatum* association and in cheatgrass communities on long-time abandoned wheatfields on the Hanford Site (Rickard *et al.* 1976). However, there is no published data on primary production in the bitterbrush cover type.

This investigation compares primary production and canopy cover on burned and unburned parts of the bitterbrush cover type during the years 1975, 1976, 1977, and 1978.

The cover type of interest because of its large extent (~70,000 a), and because unlike most semi-arid rangelands in Washington, it has not been grazed by livestock since 1943. It is expected that the land will not be used for livestock grazing in the future but will be used as industrial sites for energy facilities such as commercial nuclear power plants (Fig. 1). These facilities will be widely spaced for safety reasons,

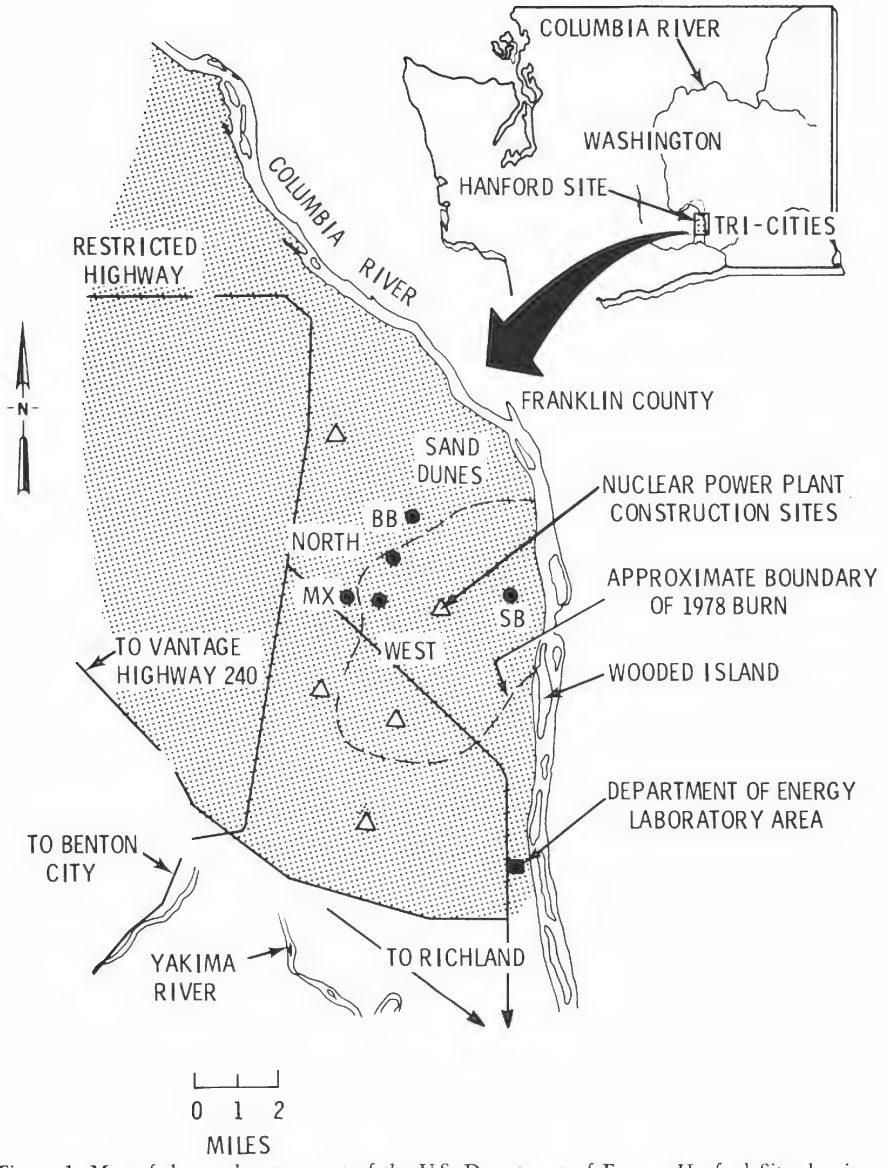


Figure 1. Map of the southeastern part of the U.S. Department of Energy, Hanford Site showing the extent of the bitterbrush-cheatgrass community, shaded area, the approximate boundaries of the 1970 burn and the location of study plots: BB = bitterbrush, MX = mixed, SB = sagebrush, North = burned site, West = burned site.

and the intervening land will probably be retained in natural vegetation. The absence of livestock grazing will likely allow for fuel (dry matter) accumulation, especially stems and leaves of cheatgrass brome; this accumulation will probably increase the incidence of wildfires in the future.

Methods Employed

Six study sites were selected for study in and adjacent to the 1970 burn (Fig. 1) but remote from industrial construction activities and transmission lines and roadways. Three sites were in parts of the community that had not been burned; these supported stands of mature shrubs. Three other sites were devoid of shrubs because of the 1970 burn.

Canopy-cover by species was measured at all study sites using Daubenmire's (1959) method of vegetational analysis. Plant names follow Hitchcock and Cronquist (1973). A 50 m long tape was read at 1 m intervals using 50—0.1 m^2 plot frames. The lines were read once in April or May at what was judged to be the peak of herbaceous plant growth. Line intercepts were used to determine the canopy cover of shrubs. Three plots each (20 x 50 m) were established, and four parallel lines at 5 m intervals were measured. All shrubs rooted in these plots were counted.

At each study site five 0.1 m^2 plots were hand-harvested of all aboveground living herbaceous phytomass. Live material was separated from dead plant material, oven dried at 50°C, and weighed. The results are expressed as grams dry weight per square meter.

Canopy Cover and Production

One of the study sites in the burned area was lost to off-road vehicular traffic in 1976. It was not replaced. All other plots remained undamaged. A summary of the herbaceous canopy cover provided by four major botanical categories is shown in Figure 2. The total canopy cover was not greatly different between burned and unburned sites but tended to be more complete on the burned sites. The low canopy cover in 1977 is attributed to the extreme drought which occurred that year. Annual grasses, mostly cheatgrass brome, dominated the canopy cover during the years 1975, 1976, and 1978. Annual forbs were the next most important contributor to canopy cover, followed in order by perennial grasses and perennial forbs. After five post fire growing seasons, the herbaceous plant cover in the burned sites was similar to that of unburned sites in species composition (except shrubs) and remained so in succeeding years. Annual forbs provided the most species over the years, and the number varied between 6 and 14 in the unburned sites and between 5 and 11 in the burned sites. There was no indication that shrubs were invading the burned sites.

A list of the vascular plant species and their individual contribution to canopy cover in the spring of 1978 is shown in Table 1. Cheatgrass brome provided most of of the canopy cover. Tansy mustard (*Descurainea pinnata*) and tumble mustard (*Sisymbrium altissimum*) dominated the canopy cover provided by annual forbs. *Poa sandbergii* was the important perennial grass. Perennial forbs contributed little to canopy cover, although they were conspicuous throughout the community because of their large, showy flowers. There was no statistically significant differences in net aboveground production between burned and unburned sites. The data were pooled and the results summarized in Table 2. The 1977 drought resulted in low plant production, only 10 $g \cdot m^{-2} \cdot yr^{-1}$. The highest production of 195 $g \cdot m^{-2} \cdot yr^{-1}$ was measured in 1975 and the average was 126 $g \cdot m^{-2} \cdot yr^{-1}$. This is near the 100 $g \cdot m^{-2} \cdot yr^{-1}$ production listed for North America shrub steppe communities (Lauenroth 1979) and is at the low end of the scale of production by grassland communities worldwide. It is

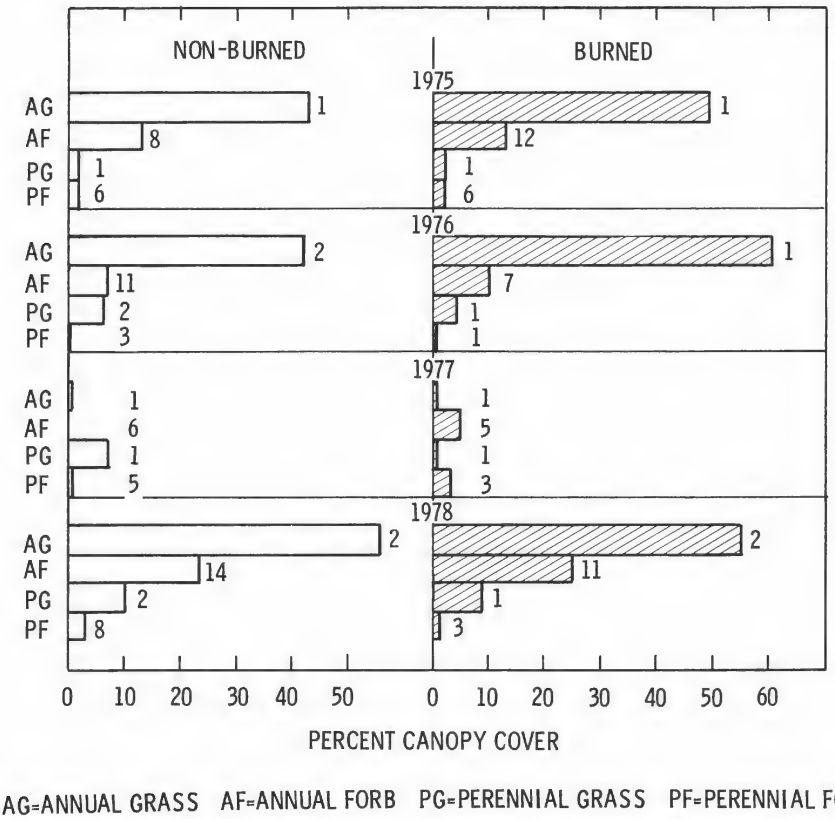


Figure 2. Percent canopy cover provided by herbaceous species during the spring of 1975, 1976, 1977, and 1978. The numerical values at the bars indicate the number of species in each botanical category.

similar to the 100 $g \cdot m^{-2} \cdot yr^{-1}$ measured in *Artemisia/Agropyron* communities (Daubenmire 1970) but less than the 240 $g \cdot m^{-2} \cdot yr^{-1}$ for cheatgrass brome communities at higher elevations with silt loam soils on the Hanford Site (Rickard *et al.* 1976). The efficiency of conversion of precipitation to dry matter averaged 11.4 g of dry matter per cm of growing season precipitation and ranged between 3.3 and 17.1 (Table 2).

Shrub Canopy Cover and Density

The three unburned shrub-dominated study sites had different amounts of shrub cover. One study site labelled SB (Fig. 1) was dominated by sagebrush. Total shrub cover was 14 percent. There were 76 sagebrush and 19 rabbitbrush shrubs on the 1000 m^2 plot. The plot labelled BB was dominated by bitterbrush and had a shrub canopy cover of

TABLE 1. Canopy cover (percent) provided by herbaceous taxa in the bitterbrush-cheatgrass community, April 1978.

Taxa	Non-Burned				Burned			All
	SB	BB	MX	$\bar{x}$	NO	WE	$\bar{x}$	$\bar{\bar{x}}$
Annual Grasses								
+Bromus tectorum	51	67	51	56	68	42	55	56
Festuca sp.	0	0	T	T	T	0	T	T
Total	51	67	51	56	68	42	55	56
Annual Forbs								
Descurainia pinnata	8	6	37	17	1	5	3	11
+Sisymbrium altissimum	15	0	0	5	11	2	6	6
°+Salsola kali	3	0	0	1	4	8	6	3
+Holosteum umbellatum	1	1	T	1	3	4	3	2
+Draba verna	T	2	0	1	T	1	1	1
Microsteris gracilis	1	1	1	1	1	3	2	1
Plantago patagonica	5	0	0	2	0	0	0	1
Amsinckia lycopsoides	T	0	T	T	0	0	0	T
°Ambrosia acanthicarpa	T	0	0	T	0	1	T	T
Cryptantha pterocarya	T	T	0	T	0	0	0	T
Phacelia linearis	0	T	0	T	0	0	0	T
Cryptantha circumscissa	0	0	T	T	0	T	T	T
Epilobium paniculatus	0	0	T	T	0	1	T	T
Layia glandulosa	0	0	T	T	0	0	0	T
Polemonium micrantha	0	0	0	0	3	T	1	1
°°+Tragopogon dubius	0	0	0	0	0	T	T	T
Total	33	10	38	28	23	25	22	26
Perennial grass								
Poa sandbergii	11	17	3	10	8	7	7	9
Stipa comata	0	1	0	T	0	0	0	T
Total	11	18	3	10	8	7	7	9
Perennial forbs								
Phlox longifolia	2	0	1	1	0	1	T	1
Oenothera pallida	0	0	6	2	0	1	0	1
Brodiaea douglasii	1	0	1	1	2	1	1	1
Crepis atrabarba	1	0	0	T	0	0	0	T
Balsamorhiza careyana	T	0	0	T	0	0	0	T
Commandra umbellatum	1	0	0	T	0	0	0	T
Psoralea lanceolata	0	0	0	0	0	T	T	T
Lomatium sp.	0	T	0	T	0	0	0	T
Astragalus sp.	0	T	0	T	0	0	0	T
Total	5	0	8	4	2	3	1	3

°Summer annual
+Introduced species
°°Biennial

T = trace amount, < 0.5
SB = Sagebrush dominant
BB = Bitterbrush dominant
MX = Mixed SB and BB
NO = North location
WE = West location

TABLE 2. Average grass and forb production and growing season (Oct.-April) precipitation, 1975 through 1978.

Year	Production $g \cdot m^{-2} \cdot yr^{-1}$	Ppt cm	Production/Ppt efficiency ratio
1975	195 ± 33	12.6	15.5
1976	159 ± 18	9.3	17.1
1977	10 ± 2	3.0	3.3
1978	139 ± 12	14.1	9.9
Average	126	9.7	11.4

± Standard error.

26 percent. There were 86 bitterbrush, seven rabbitbrush, and only two sagebrush shrubs on this plot. The plot labelled MX had about equal amounts of sagebrush and bitterbrush shrubs, and together provided 22 percent of the total shrub cover. *Eriogonum niveum*, a small subshrub, provided an additional 15 percent canopy cover for a total

shrub canopy of 37 percent. There were 51 bitterbrush, 59 sagebrush, and 627 *E. niveum* shrubs on this plot.

No attempt was made to estimate the annual production by shrubs. Mack (1976) estimated the annual litterfall of a sagebrush community on the Hanford Site at 12 $g \cdot m^{-2} \cdot yr^{-1}$, and this value is probably valid for our sites as well.

It appears that the presence of mature shrubs had little influence on herbage production. The shrubs probably exploit soil water that penetrates deeply into the sandy soil, whereas the herbs, especially cheatgrass brome, exploits shallow penetrating soil water. Cline and Rickard (1977) report that cheatgrass was not very effective at exploiting soil water that had penetrated below 0.5 m deep. Sagebrush has an extensive root system that can penetrate to depths of 2 m (Sturges 1977). How long a time will pass before shrubs re-colonize the burn is unknown. Daubenmire (1976) reports that abandoned wheatfields colonized by cheatgrass brome have resisted invasion by native species for 50 years. Fires also influence the ability of shrubs to occupy the land because sagebrush and bitterbrush are easily killed by fire and do not sprout vegetatively after burning.

Wildlife Implications

Reinvasion of burned areas by bitterbrush and sagebrush is restricted to self-established seedlings. Of these two species, bitterbrush would be the choice of wildlife managers because it provides browse for mule deer, which are a part of the fauna of the Hanford Site (Hedlund 1975); they range throughout the bitterbrush cover type. Increased incidents of fire could dramatically reduce the amount of browse available to mule deer by eliminating bitterbrush shrubs from large land areas. This could be important because the land surrounding the Hanford Site is largely in agricultural use, and crop damage by deer is not generally tolerated by land owners. At the present time crop damage by deer on croplands east of the Columbia River is believed to be very small.

Acknowledgments

Work performed in part under contract number DE-AC06-76RL0-1830 with the U.S. Department of Energy and with the Washington Public Power Supply System, Richland, Washington.

Literature Cited

Cline, J. F., D. W. Uresk, and W. H. Rickard. 1977. Comparison of soil water used by a sagebrush-bunchgrass and a cheatgrass community. J. Range Mgmt. 30:199-201.

Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. Northw. Sci. 33:43-64.

———. 1970. Steppe Vegetation of Washington. Wash. Agr. Expt. Sta. Tech. Bull. 62.

———. 1976. Plant succession on abandoned fields and fire influences in a steppe area in southeastern Washington. Northw. Sci. 49:36-48.

Hedlund, J. D. 1975. Tagging mule deer fawns in south-central Washington. Northw. Sci. 49: 253-260.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. of Wash. Press, Seattle.

Lauenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective, *in* Perspectives in Grassland Ecology. N. R. French (ed.). Springer-Verlag, N.Y.

Mack, R. N. 1977. Mineral return via the litter of *Artemisia tridentata*. Am. Medl. Nat. 97:189-197.

Rickard, W. H., D. W. Uresk, and J. F. Cline. 1976. Productivity Response to Precipitation by Native and Alien Plant Communities. Proceedings of the Symposium on Terrestrial and

Aquatic Ecological Studies of the Northwest. Sponsored by the Northwest Scientific Association. Eastern Wash. State College Press.
Sturges, D. C. 1977. Soil water withdrawal and root characteristics of big sagebrush. Am. Midl. Nat. 98:257-274.

Received March 27, 1980
Accepted for publication June 10, 1980

Publication Announcement

Forest Succession and Stand Development Research in the Northwest

Proceedings are now available of the above-titled symposium held 26 March 1981 as part of the Northwest Scientific Association annual meeting at Oregon State University, Corvallis. The symposium was co-sponsored by the Northwest Scientific Association, USFS Pacific Northwest Forest and Range Experiment Station, and Oregon State's School of Forestry.

Papers in the proceedings have all received peer review and will be valuable resources for persons interested in these topics. Joseph E. Means is the editor of this 170-page bound volume.

The symposium had three goals: focus attention on the fields of forest succession and stand development as tools for basic research and valuable sources of information for managers, provide a sampling of and an entree into research in these fields in the Northwest, and seek to stimulate further work in these fields. Between the introductory paper on "Patterns of Development of Forest Stands" and the concluding paper on "Forest Succession Research in the Northwest" are 11 papers on Forest Succession and 5 papers on Stand Development.

The cost of this publication is $6.00 and may be obtained from:

Forest Research Laboratory
Oregon State University
Corvallis, Oregon 97331

Errata

Helvey, J. D., and W. B. Fowler. Precipitation variability in the Columbia Basin of Washington, pp. 27-33 Northwest Science 56(1).

Page 29: Regression equation should read

Precipitation (cm) = 13.25 + 0.0247 (elevation m)

Page 31, Figure 2: Equation should read

$Y = 13.25 + 0.0247X$

$r^2 = 0.47$

Van Vuren, D., and S. E. Thompson, Jr. Opportunistic feeding by coyotes, pp. 131-135 Northwest Science 56(2).

Page 131: First sentence of abstract should read

Opportunistic feeding by coyotes (*Canis latrans*) was evaluated by relating the diet of three coyotes during one year to prey availability.

Page 131: Present address of D. Van Vuren is Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045.

Page 132: The first word of line 16 should read

To

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian D. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Andrew V. Corry
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
F. A. Gilfillan
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Frank D. Nicol
William A. Rockie
Francis J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
S. C. Vandecaveye
Richard B. Walker
D. J. Wort

1982 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1982 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Gonzaga University, Spokane, Washington
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Malaspina College, Nanaimo, British Columbia, Canada
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Northern Montana College, Havre, Montana
Oregon College of Education, Monmouth, Oregon
Oregon Institute of Technology, Klamath Falls, Oregon
Oregon State University, Corvallis, Oregon
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
Saint Martin's College, Lacey, Washington
Seattle Central Community College, Seattle, Washington
Seattle Pacific University, Seattle, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
South Seattle Community College, Seattle, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Oregon, Eugene, Oregon
University of Puget Sound, Tacoma, Washington
University of Victoria, Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State University, Pullman, Washington
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Yakima Valley College, Yakima, Washington

1982 Sustaining Individual Members

Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Robert L. Carr, Cheney, Washington
Susan G. Conrad, Corvallis, Oregon
George W. Douglas, Victoria, British Columbia, Canada
Bruce Ettling, Vancouver, Washington
George R. Fahnestock, Seattle, Washington
Gerald H. Haddock, Wheaton, Illinois
Frederick C. Hall, Portland, Oregon
Charles R. Hatch, Moscow, Idaho
Robert J. Jonas, Pullman, Washington
Barry L. Keller, Pocatello, Idaho
Denis L. Lavender, Corvallis, Oregon
William L. Lester, Arcata, California
William A. Long, Crescent City, California
Albert L. Merkel, Moscow, Idaho
Daniel F. Milam, Bellevue, Washington
Emmett B. Moore, Jr., Richland, Washington
Milton A. Mosher, Pullman, Washington
William A. Rickard, Richland, Washington
Lee E. Rogers, Richland, Washington
Raymond A. Soltero, Cheney, Washington
Ronald J. Taylor, Bellingham, Washington
Daniel W. Uresk, Rapid City, South Dakota
Shepard M. Zedaker, Christiansburg, Virginia

Northwest Science

Washington State University

Pullman, Washington 99164

ber
De & Env. Engineering
Was e University
Pu 164

Associate Editors

Botany	Kenneth C. Swedberg	Eastern Washington University
Forestry	Arthur R. Tiedemann	U.S. Forest Service
Geology	Franklin F. Foit, Jr.	Washington State University
Soils	Stanley P. Gessel	University of Washington
Zoology	Irven O. Buss	Washington State University

Change of Address Send change of address notice to the Treasurer as listed on the inside front cover.

Instructions to Authors The pages of Northwest Science are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. At least one of the authors of papers submitted for publication must be a member of the Northwest Scientific Association. Manuscripts (original typescript plus two copies) should be submitted to the Editor, Northwest Science, Washington State University, Pullman, Washington. Prior to submitting manuscripts, authors should request a copy of "Instructions to Authors" from the Editor.

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164, U.S.A.

Volume 56, Number 4

November 1982

Northwest Science

259 Early Cenozoic Geology of Central Washington State: II. Implications for Plate Tectonics and Alternatives for the Origin of the Chiwaukum Graben
Randall L. Gresens

268 A Rapid Method for Analysis of Tissues for Heavy Metals Utilizing Atomic Absorption Spectrophotometry
Ronald J. Kendall and Patrick F. Scanlon

268 Taxonomic Extensions in the Chilcotin Mountains of Southern British Columbia
Corinne J. Selby and Michael D. Pitt

276 Soil Nitrogen Gradients as Influenced by Sagebrush Canopy in Southern British Columbia
S. J. Wikeem and Michael D. Pitt

287 A Preliminary Survey of Forest Bird Communities in Northern Idaho
Steven R. Peterson

299 Mule Deer and Elk Responses to Horsefly Attacks
William B. Collins and Philip J. Urness

303 Summer Raptor Populations of a Washington Coulee
Richard L. Knight and Dwight G. Smith

310 Winter Foods of Eastern Oregon Bobcats
Dale E. Towell

316 Comparison of Phenological Patterns in Prairie and Subalpine Meadow Communities
Louise E. Jackson

329 Organochlorine Residues in Bats after a Forest Spraying with DDT
Charles J. Henny, Chris Maser, John O. Whitaker, Jr., and T. Earl Kaiser

Official Publication of the Northwest Scientific Association

US ISSN 0029 344X

Northwest Science

Volume 56, Number 4, November 1982

The Northwest Scientific Association is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to Northwest Science, is open to individual persons for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 3000 students or more, $40. All other subscribers, $20 per year. Sustaining membership, $25 per year for individual persons and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Payment should be made to the Treasurer.

Editor **John W. Weber**
Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164-2910

Officers of the Association

President **John H. Perkins**
The Evergreen State College
Olympia, Washington (1983)

Vice-President **Stephen F. Arno**
USDA Forest Service
Missoula, Montana (1983)

Secretary **Robert L. Carr**
Eastern Washington University
Cheney, Washington (1984)

Treasurer **Robert J. Jonas**
Department of Zoology
Washington State University
Pullman, Washington 99164-4220
(1983)

Past President **James R. Chambers**
Walla Walla College
College Place, Washington (1982)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Black
University of British Columbia
Vancouver, British Columbia
(1985)

Charles R. Hatch
University of Idaho
Moscow, Idaho (1983)

Janet E. Hohn
U.S. Fish and Wildlife Service
Portland, Oregon (1983)

Denis P. Lavender
Oregon State University
Corvallis, Oregon (1984)

Roger del Moral
University of Washington
Seattle, Washington (1983)

Don Minore
U.S. Forest Service
Corvallis, Oregon (1984)

Richard J. Naskali
University of Idaho
Moscow, Idaho (1984)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

Ronald H. Sauer
Battelle Northwest Laboratories
Richland, Washington (1984)

Steven R. Seavey
Lewis and Clark College
Portland, Oregon (1985)

Kareen Sturgeon
Linfield College
McMinnville, Oregon (1985)

J. Mary Taylor
2718 SW Old Orchard Road
Portland, Oregon 97201
(1983)

Robert Zasoski
University of Washington
Seattle, Washington (1984)

Donald B. Zobel
Oregon State University
Corvallis, Oregon (1983)

*Term of office expires in the year given in parentheses

PUBLISHED QUARTERLY BY WASHINGTON STATE UNIVERSITY PRESS
WITH COLLABORATION OF NORTHWEST SCIENTIFIC ASSOCIATION

Randall L. Gresens

Department of Geological Sciences
University of Washington
Seattle, Washington 98195

Early Cenozoic Geology of Central Washington State: II. Implications for Plate Tectonics and Alternatives for the Origin of the Chiwaukum Graben

Abstract

Reconstruction of tectonic events of central Washington prior to about 50 mybp is tenuous. The early Eocene Swauk Formation may have been deposited after a period of tectonic quiescence. Folding of Swauk on E-W axes between 51-47 mybp cannot be readily correlated with presumed plate motions. Coeval emplacement (at 47-48 mybp) of two tensional dike swarms (Teanaway and Corballey Canyon), of contrasting lithologies and extensional directions, presents a tectonic paradox that is not easily solved. The paradox may be resolved by assuming sufficient right-lateral strike-slip motion on the east-bounding fault of the Chiwaukum graben (the Entiat fault) so that the counterpart of the Teanaway dikes lies somewhere southeast below the Columbia Plateau. Two models for development of the Chiwaukum graben from about 46 to 40 mybp by strike-slip motion are possible. The first requires a wedge-shaped graben; this is the "ball-bearing" model that reconciles the Chiwaukum graben with documented clockwise rotation of Eocene rocks that lie to the west. A preferred model for the graben is as a rhombochasm ("pull-apart" structure), such as has been proposed for Tertiary basins of California. By this model, a primary kink in a strike-slip fault opens into a diamond-shaped depression during active movement. The exposed Chiwaukum graben is thus interpreted as the northern end of a rhombochasm that projects beneath the Columbia Plateau. Cessation of graben activity at about 40 mybp agrees with the end of Laramide deformation over western North America, and it is correlated with global reorganization of plate motions. A period of tectonic and magmatic quiescence from 40-34 mybp correlates with development of a major erosion surface over western North America during plate reorganization. Deformation of the Wenatchee Formation during 34-29 mybp marks the onset of renewed techonism and magmatism as subduction was initiated in the Pacific Northwest. Deformation of the southern part of the Chiwaukum graben by right-lateral shearing and associated emplacement of the Horse Lake Mountain complex may be related to the initiation of strike-slip motion elsewhere along the Pacific margin as the spreading center between the Farallon and Pacific plates encountered a subduction zone at the continental margin. Erosional stripping of the Wenatchee Formation in the region now occupied by the Cascade Range occurred before deposition of the Columbia River Basalt Group in Miocene time and may mark the beginning of the ancestral Cascades.

Introduction

Carlson (1976) correlated Cenozoic plate motions with the geology of the continental margin of the Pacific Northwest (Coast Range and Puget-Willamette Lowland) and the Cascade Range of Washington-Oregon. The summary of geologic history presented in Part I (Gresens 1982) supplements the correlation of plate motion with the geology of the central Cascade Range of Washington.

Plate Tectonic Implications

Early Eocene

The lateritic paleosol present at the base of the Swauk Formation and the probable widespread occurrence of the unit suggest that it may have been deposited on an erosion surface developed during a time of tectonic and magmatic quiescence. It is difficult to attempt correlation with plate motions because the age of the presumed

erosion surface is not well documented, lying between 88 my (age of the Mt. Stuart granodiorite; Engels and Crowder 1971) and somewhat less than the 51 my age of upper Swauk Formation (Tabor and Frizzell 1977). Erickson (1976) used fission-track apparent ages and annealing temperatures of apatite to suggest that the Mt. Stuart batholith was uplifted and unroofed at 55 ± 6 mybp. This date could reflect the onset of renewed tectonism after a period of crustal stability, but considerable uncertainty remains.

East-west fold axes, suggestive of N-S compression, pre-date Teanaway Basalt and therefore were formed in the interval of about 51-47 mybp (Gresens 1979, Ewing 1980). This compressive direction does not fit well into a plate tectonic model. During the Cretaceous and into the early Tertiary, the Kula plate was moving northward with respect to the Pacific plate (Hayes and Pitman 1970) as the Pacific plate itself was moving northward relative to a presumably fixed "hot-spot" (Clague and Jarrard 1973). Interaction of either plate with North America could produce N-S compression and E-W fold axes. However, North America, moving relatively westward, was presumably interacting with the Farallon plate moving relatively eastward (Atwater 1979, Hayes and Pitman 1979); these movements should have produced N-S fold axes. It is possible that this area was involved in crustal rotation, as observed for Eocene rocks to the west and southwest (Simpson and Cox 1977, Beck 1976), so that they no longer reflect the true direction of tectonic stresses during early Eocene folding.

Armstrong (1978), Vance (1979), and Ewing (1980) suggested that a broad NW-SE subduction-related magmatic arc, the Challis arc, was active in early and middle Eocene time in British Columbia, Washington, central Oregon, Idaho, Montana, and Wyoming. Much of the igneous activity of the Chiwaukum graben area, including the Teanaway Basalt and the Corbaley Canyon dike swarm, would be included in Challis volcanism. Definition of the magmatic arc is based on regional plots of occurrences of plutonic or volcanic rocks and their ages. Failure to examine the tectonic setting and the tectonic implications of the petrology of individual occurrences leads to over-simplification in broad overviews of this type. For example, the Corbaley Canyon tensional bimodal dike swarm is better explained by deep crustal rifting than by a subduction mechanism.

Ewing (1980) attempted to explain E-W fold axes in the Swauk Formation and the NE trend of the tensional Teanaway dikes by a single stress regime having a principal stress direction oriented slightly east of north. The change from north-south compression to WNW-ESE extension was presumed to reflect an exchange of the intermediate and least principal stresses at about 47 mybp. But such an exchange should produce NNW dextral or NNE sinistral strike-slip faults, not the extensional rifting indicated by the Teanaway dikes. Clearly, much work remains before a definitive correlation between early Eocene plate motions and igneous and tectonic events is possible for this region.

Middle Eocene

The Chiwaukum graben became active immediately after or during the close of the early Eocene events. Geologists familiar with the Pacific Northwest have long speculated informally on the possibility of strike-slip motion on the Entiat fault, and the suggestion was recently formalized (Gresens 1979, Ewing 1980). There is no evidence that the

fault existed prior to about 46 mybp. Features suggestive of strike-slip movement include (1) the linearity of the fault, (2) the failure of the Jurassic ultramafic rocks to appear east of the Chiwaukum graben, and (3) the failure of the NE-trending Teanaway dike swarm to appear east of the Chiwaukum graben. Ewing (1980) considered the Entiat to be part of a network of strike-slip faults that were active in the Eocene.

The new radiometric dates obtained during this investigation emphasize another geologic incompatibility across the Entiat fault. The Teanaway and Corbaley Canyon dike swarms are essentially coeval. Yet they represent markedly different compositions and crustal extension in directions nearly 90° apart, even though they are geographically only 50 km apart. These observations present a fundamental tectonic problem if they are in their original positions with respect to each other. Two possibilities for the origin of the graben, each calling for strike-slip motion on the Entiat fault, are presented.

Model One—Rotation and Strike-slip Movement

Figure 1a shows the outline of the graben. There is a basic wedge shape, although the irregular Leavenworth fault zone must be given a "best fit." Figure 1c shows the schematic development of the graben by a combination of strike-slip motion and clockwise rotation. Although the wedge shape could be explained by rotation alone, restoration of the rotation would make the Teanaway-Corbaley paradox an even greater tectonic problem (Fig. 1b).

Clockwise rotation of crustal rocks of Eocene age along the Oregon and Washington coasts is well documented by paleomagnetic data (Beck 1976, Simpson and Cox 1977, Globeman 1979, Beck and Burr 1979). It could be argued that there must be a transition, either gradually over a broad zone or abruptly over a narrow zone, from the marginal part of the continent that is strongly affected by rotation into the stable continental interior that has not been rotated. The Entiat fault zone and the Chiwaukum graben could be an abrupt transitional area. This model follows the "ball-bearing" model for combined right-lateral strike-slip motion and clockwise rotation as proposed by Beck (1976).

Model Two—Rhombochasm

The geometry of the Chiwaukum graben also lends itself to interpretation as a rhombochasm (Carey 1958), with the southern half covered by the Columbia River Basalt Group (Fig. 1d). This model does not require a rotational component, but merely strike-slip motion along a fault having an original "kink." This is, for example, a plausible model for the origin of late Cenozoic basins of California (Crowell 1974). The Chiwaukum graben has the correct geometry for this type of "pull-apart basin" as defined by Crowell. The side bounded by strike-slip movement is straight (Entiat fault), whereas the tensionally rifted "kink" boundary is irregular (Leavenworth fault).

Either of these models would explain the mismatch of geology across the Chiwaukum graben and would alleviate the tectonic paradox posed by the coeval Teanaway and Corbaley dike swarms; sufficient separation by restoration of strike-slip movement might make separate stress regimes plausible. Either model would allow the gradual opening of a depression that could ultimately accommodate 5800 m of Chumstick sediment. The author prefers the second model, but either is possible. The models differ in terms of the possibility of differential rotation across the graben, but this may be tested by

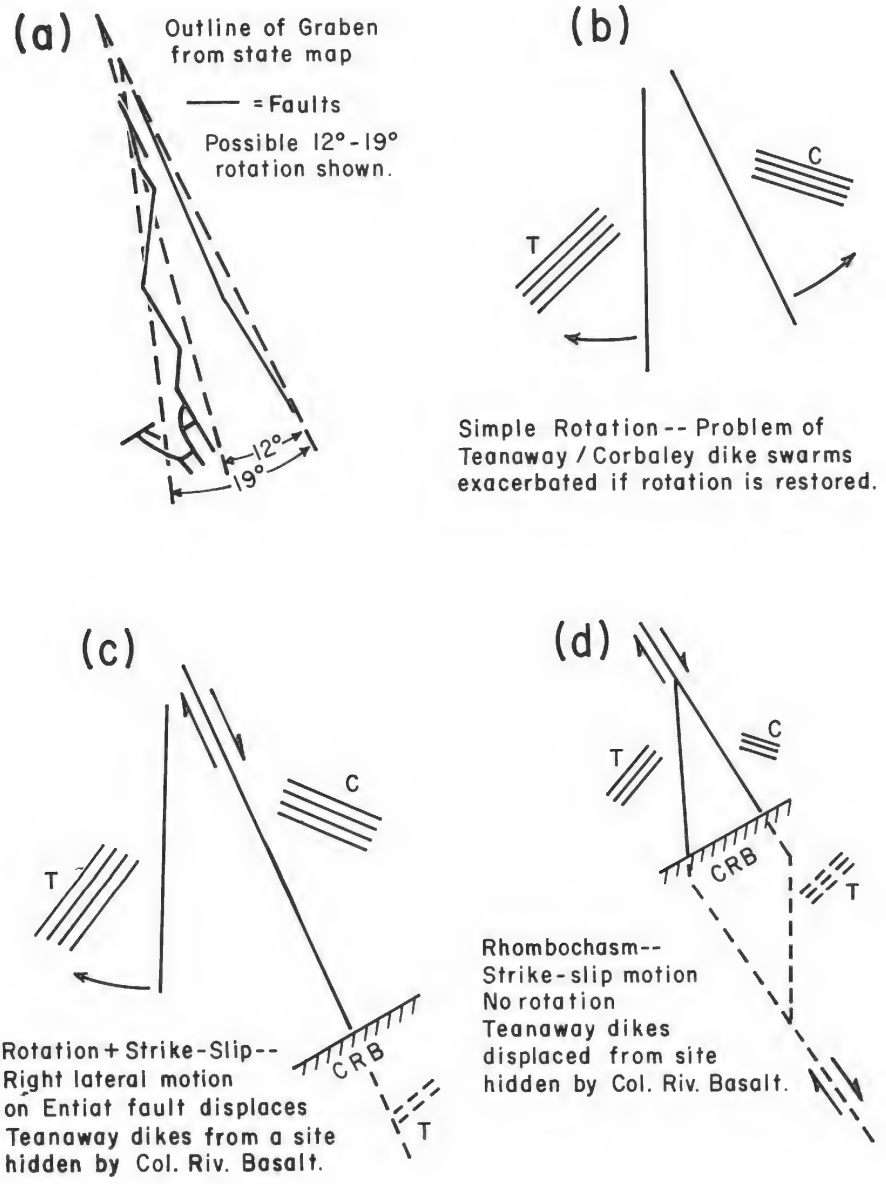


Figure 1. Possible origins for the Chiwaukum graben. "T" and "C" on the diagrams indicate the Teanaway and Corbaley Canyon dike swarms, respectively. "CRB" refers to Columbia River Basalt group, which covers the southern projection of the Chiwaukum graben. Further explanation in the text.

paleomagnetic work on the Teanaway Basalt and Corbaley Canyon rocks. The required paleomagnetic work is now in progress (M. Beck, pers. comm., 1979, 1980).

Late Eocene-Early Oligocene

The Chiwaukum graben became inactive at about 40 mybp, and a period of tectonic quiescence ensued. This period coincides with the end of Laramide deformation over the entire western Cordillera, which is in turn correlated with changes in motion of the North American and Pacific plates (Coney 1971, 1972; Epis and Chapin 1975; Gresens 1978, 1980) and probably with a global reorganization of plate motion during the Eocene (Rona and Richardson 1978; Gresens, in press).

Late Oligocene

Post-34 mybp compression of the region must correlate with renewed tectonism and magmatism over much of the western Cordillera at about 35 mybp (Epis and Chapin 1975) and, more specifically, with the renewal of subduction in the Pacific Northwest (Vance 1979). Compressive stress was transmitted to the continental interior.

The spreading center between the Pacific plate and the Farallon plate encountered a subduction zone at the western margin of North America at about 29 mybp (Atwater 1979), and this initiated right-lateral strike-slip deformation at the continental margin near San Francisco. The passive emplacement of the 29 my Horse Lake Mountain complex is associated with right-lateral strike-slip motion, and it is suggested that this may be a more northerly expression of renewed strike-slip motion on the North American continent (Gresens 1980). Central Washington is admittedly rather far from San Francisco, but the timing and sense of motion coincide.

Concluding Remarks

The part of the North American continental margin now represented by the state of Washington has a long history of right-lateral strike-slip faulting, including the late Creataceous (Davis *et al.* 1978) as well as the middle Eocene and late Oligocene events described above. These apparently are interspersed with "conventional" continental margin subduction and related igneous activity and with at least one period of tectonic quiescence. The writer appreciates that correlations may be revised as new data become available. However, any regional tectonic synthesis must take into account the factual chronology of geologic events presented in Part I of this paper.

Acknowledgments

Support for field work was obtained from the division of Geology and Earth Resources, State of Washington Department of Natural Resources. Potassium-argon dates were obtained under National Science Foundation Grant Number EAR76-21308, and fission track dates were obtained courtesy of Joseph A. Vance.

Literature Cited

Armstrong, R. L. 1978. Cenozoic igneous history of the U.S. cordillera from lat. 42° to 49°N, pp. 265-282 *in* Smith, R. B., and G. P. Eaton (eds.). Cenozoic Tectonics and Regional Geophysics of the Western Cordillera. Geol. Soc. Amer. Mem. 152.

Atwater, Tanya. 1970. Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. Geol. Soc. Amer. Bull. 81: 3513-3535.

Beck, M. E., Jr. 1976. Discordant paleomagnetic pole positions as evidence of regional shear in the western cordillera of North America. Am. Jour. Sci. 276: 694-712.
———, and C. D. Burr. 1979. Paleomagnetism and tectonic significance of the Goble Volcanic Series, southeastern Washington. Geology 7: 175-179.
Carey, S. W. 1958. The tectonic approach to continental drift, pp. 177-355 *in* Carey, S. W. (ed.). Continental Drift. Univ. Tasmania Geology Department Symposium No. 2.
Carlson, R. L. 1976. Cenozoic Plate Convergence in the Vicinity of the Pacific Northwest, a Synthesis and Assessment of Plate Tectonics in the Northeastern Pacific, Univ. Washington, Ph.D. thesis.
Claque, D. A., and R. D. Jarrard. 1973. Tertiary Pacific plate motion deduced from the Hawaiian-Emperor chain. Geol. Soc. Amer. Bull. 84: 1135-1154.
Coney, P. J. 1971. Cordilleran tectonic transitions and motions of the North American plate. Nature 233: 462-465.
———. 1972. Cordilleran tectonics and North America plate motion. Am. Jour. Sci. 272: 603-628.
Crowell, J. C. 1974. Origin of Late Cenozoic basins in southern California, pp. 190-204 *in* Dickinson, W. R. (ed.), Tectonics and Sedimentation. Soc Econ. Paleontol. and Mineral Spec. Pub. No. 22.
Davis, G. A., J. W. H. Monger, and B. C. Burchfiel. 1978. Mesozoic construction of the Cordilleran "collage" central British Columbia to central California, pp. 1-32 *in* Howell, D. C., and K. A. McDougall (eds.). Mesozoic Paleogeography of the Western United States. Soc. Economic Paleontologists & Mineralogists, Pacific Sec.
Engels, J. C., and D. F. Crowder. 1971. Late Cretaceous fission-track and potassium-agron ages of the Mount Stuart granodiorite and Beckler Peak stock, north Cascades, Washington. U.S. Geol. Surv. Prof. Pap. 750-D: D39-D43.
Epis, R. C., and C. E. Chapin. 1975. Geomorphic and tectonic implications of the post-Laramide, late Eocene erosion surface in the southern Rocky Mountains, pp. 45-74 *in* Curtis, B. F. (ed.). Cenozoic History of the Southern Rocky Mountains. Geol. Soc. Amer. Mem. 144.
Erikson, E. H., Jr. 1976. Implications of apatite fission track ages in the Mount Stuart batholith, Cascade Mountains, Washington (abs.). Geol. Soc. Amer., Abstracts with Programs 8: 372.
Ewing, T. E. 1980. Paleogene tectonic evolution of the Pacific Northwest. Jour. Geology 88: 619-638.
Globerman, B. R. 1979. Geochemistry of Eocene basalts from the Black Hills, Washington Coast Range (abs.). Geol. Soc. Amer., Abstracts with Programs 11: 80.
Gresens, R. L. 1978. Regional significance of a late Eocene/early Oligocene erosion surface exposed in central Washington State (abs.). Geol. Soc. Amer., Abstracts with Programs 10: 107.
———. 1979. Timing of Cenozoic igneous and tectonic events on the eastern flank of the Cascade Range in central Washington (abs.). Geol. Soc. Amer., Abstracts with Programs 11: 80.
———. 1980. Deformation of the Wenatchee Formation and its bearing on the tectonic history of the Chiwaukum graben, Washington, during Cenozoic time. Geol. Soc. Amer. Bull. 91: 4-7 (Part I), 115-155 (Part II).
———. 1982. Early Cenozoic geology of central Washington State: I. Summary of sedimentary, igneous, and tectonic events. Northw. Sci. 56: 218-229.
———. In press. Extension of the telluride erosion surface to Washington State, and its regional and tectonic significance. Tectonophysics.
Hayes, D. E., and W. C. Pitman III. 1970. Magnetic lineations in the North Pacific, pp. 291-314 *in* Hayes, J. D. (ed.). Geological Investigations of the North Pacific. Geol. Soc. Amer. Mem. 126.
Rona, P. A., and E. S. Richardson. 1978. Early Cenozoic global plate reorganization. Earth and Plan. Sci. Ltrs. 40: 1-11.
Simpson, R. W., and A. Cox. 1977. Paleomagnetic evidence for tectonic rotation of the Oregon Coast Range. Geology 5: 585-589.
Tabor, R. W., and V. A. Frizzell, Jr. 1977. Tertiary stratigraphy of the central Cascades Mountains, Washington State. Part II. Stratigraphy of the Swauk, Silver Pass, Teanaway, and Roslyn Formations, pp. 88 -100 *in* Brown, E. H., and R. C. Ellis (eds.). Geological Excursions in the Pacific Northwest. Bellingham, Western Washington Univ. Press.
Vance, J. A. 1979. Early and middle Cenozoic arc magmatism and tectonics in Washington State (abs). Geol. Soc. Amer., Abstracts with Programs 11: 132.

Received May 20, 1981
Accepted for publication July 17, 1981

Ronald J. Kendall[1]

and

Patrick F. Scanlon

Department of Fisheries and Wildlife Sciences
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061

A Rapid Method for Analysis of Tissues for Heavy Metals Utilizing Atomic Absorption Spectrophotometry

Abstract

A rapid analytical technique for analyzing heavy metals in tissue samples is described. The technique utilizes Corning glass ignition tubes which are used as a container for storing, ashing, and digestion of samples. This process reduces the amount of glassware needed in the analytical procedure, reduces exposure of samples to contamination by excessive glassware use, and provides the analyst with a clean, economical, and efficient system for measuring heavy metals in animal tissues.

Introduction

Numerous studies in our laboratory dealing with heavy metal contamination in the environment (Scanlon 1979, Scanlon *et al.* 1979, Scanlon *et al.* 1980, Kendall and Scanlon 1979, Kendall 1980) have necessitated development of a rapid analytical technique for heavy metal measurements (i.e., lead (Pb), cadmium (Cd), nickel (Ni), zinc (Zn), and copper (Cu)) in animal tissues. Although large numbers of samples are processed, individual handling of each sample is of utmost importance so as to avoid contamination and maintain identity. For this reason, a tissue processing technique was developed utilizing Corning glass ignition tubes for ashing of samples prior to analysis by atomic absorption spectrophotometry. The present report describes our technique for drying, ashing, digestion, and analysis of tissue samples for heavy metals by atomic absorption spectrophotometry.

Methods and Materials

Preparation of laboratory glassware was an important consideration in the heavy metal measurements. Before use, glassware was soaked (> 24 hr) and washed in 5 percent Lakeseal Laboratory Glassware Cleaner (Peck's Products, St. Louis, Mo.) and rinsed in distilled-deionized H_2O. Glassware was then leached in 20 percent HNO_3 (> 24 h) and rinsed in distilled-deionized H_2O before usage. Glassware was then transferred to a 5 percent HNO_3 solution (> 24 h), rinsed in distilled-deionized water, and stored in a clean cabinet. All clean glassware was placed in a 5 percent HNO_3 bath at least 24 h prior to use and rinsed 9-10 times with deionized water.

All tissue samples were dissected free using acid-washed stainless steel surgical instruments. Plastic gloves were worn throughout this procedure. Tissue samples were

[1]Present address: Huxley College of Environmental Studies, Western Washington University, Bellingham, Washington 98225.

then placed in acid-washed sample vials, covered with parafilm, frozen, and later lyophilized at –50° C for 24 h. After lyophilization, all samples were placed in a dessication chamber to prevent rehydration and possible contamination. Tissue samples were then added to tared 16 x 125 mm ignition tubes (glass etched with numbering system) and weighed to the nearest 0.10 mg. Samples were then ashed overnight in a muffle furnace (500° C) and the ash brought into solution in distilled-deionized H_2O (Barnstead Demineralizer)/HNO_3 (reagent grade, Fisher Scientific)/HCl (reagent grade, Fisher Scientific). An automatic repipette system (20 ml) was used to maintain precision in acid delivery. Samples were allowed to digest, and the ignition tubes were capped with parafilm and centrifuged for 5 min. at 761 g. Appropriate dilutions were made, and heavy metal concentrations were measured in tissues using an Instrumentation Laboratories Model 351 atomic absorption spectrophotometer (Wilmington, Mass.). Automatic background correction was accomplished with a deuterium continuum light source; unknown samples were attained from a standard curve.

Water pollution quality control samples for trace metal analyses were obtained from the Environmental Monitoring and Support Laboratory, Environmental Protection Agency, Cincinnati, Oh. These samples were used to verify and standardize analytical procedures in addition to bovine liver standards obtained from the National Bureau of Standards, Washington, D.C.

Standards were made up in 100 ml acid-washed pyrex volumetric flasks. New standards were routinely checked against old standards. Standard additions were used to check for matrix interferences. Spiked samples were run to obtain percent recovery. Blank tubes were routinely run through the procedure to check for contamination. Deionized water and acids used were analyzed by flameless atomic absorption spectrophotometry to check for metallic contamination. Lead concentrations were calculated in terms of μg lead/g dry weight of tissue.

Results and Discussion

Using this technique, one has the capability of analyzing upwards of 300 different tissue samples per week for various heavy metals. A slow point in the process is the weighing out of samples in the ignition tubes by a Mettler balance. We suggest use of a 5 decimal place analytical top-loading balance to facilitate getting samples weighed out. This technique should speed up the process considerably.

In the past, the process has often been slowed by the use of porcelain crucibles for ashing, requiring excessive space in the furnace. However, use of ignition tubes circumvents this problem, as many ignition tubes can be stacked horizontally (approximately 10 degree tilt) in the furnace. Care must be exercised, however, in placing the ignition tubes in a cool furnace and bringing the temperature up slowly (room temperature to 500° C in about 5 hr) to avoid having samples boil out of tubes which may occur if the temperature is increased too rapidly.

Samples can be stored in the tubes before ashing if parafilm is used for sealing the tube. Sample storage can also be facilitated by use of test tube racks where a large number of samples can be stored in a small area.

Literature Cited

Kendall, R. J., and P. F. Scanlon. 1979. Lead concentrations in mourning doves collected from middle Atlantic game management areas. Proc. Southeastern Assoc. Fish Wildl. Agencies 33:165-172.

———. 1980. The Toxicology of Lead Shot and Environmental Lead Ingestion in Avian Species with Emphasis on the Biological Significance in Mourning Dove Populations. Virginia Polytechnic Institute and State Univ., Blacksburg, Ph.D. thesis.
Scanlon, P. F. 1979. Lead contamination of mammals and selected invertebrates near highways of different traffic volumes, pp. 200-208 *in* Symposium Pathobiology Environmental Pollutants: Animal models and wildlife as monitors. National Research Council, National Academy of Sciences.
———, T. G. O'Brien, N. L. Schauer, J. L. Coggins, and D. E. Steffen. 1979. Heavy metal levels in feathers of wild turkeys from Virginia. Bull. Environ. Contam. Toxicol. 21:591-595.
———, V. D. Stotts, R. G. Oderwald, T. J. Dietrick, and R. J. Kendall. 1980. Lead concentration in Maryland waterfowl with and without ingested lead shot present in gizzards. Bull. Environ. Contam. Toxicol. 25:855-860.

Received March 26, 1981
Accepted for publication May 5, 1981

Corinne J. Selby

Plant Ecologist, B.C. Pedology Unit
Agriculture Canada Research Station
6660 N.W. Marine Drive
Vancouver, British Columbia V6T 1X2

and

Michael D. Pitt

Department of Plant Science
University of British Columbia
Vancouver, British Columbia V6T 2A2

Taxonomic Extensions in the Chilcotin Mountains of Southern British Columbia

Field studies in 1977 revealed disjunct populations for several plant species in British Columbia. *Cinclidium stygium* Sw., *Erigeron purpuratus* Greene, and *Ranunculus inamoenus* Greene all occurred 350 to 450 km beyond previously documented populations. Other disjunct populations of *Lupinus lepidus* Dougl. var. *lobbii* (Gray) Hitchc., *Papaver lapponicum* (Tolm.) Nordh. subsp. *occidentale* (Lundstr.) Knaben, and *Ranunculus gelidus* Kap. & Ker. were identified as rare, although not currently endangered in British Columbia.

Introduction

During the summer of 1977, studies began on the alpine and subalpine vegetation found in the Chilcotin Mountain rangelands of British Columbia (Selby 1980). During this work, 239 sites were sampled to produce an extensive collection of all vascular plants, bryophytes and macrolichens. Because of relative inaccessibility, this region of British Columbia has not previously benefited from intensive botanical surveys. As cattle grazing is a major use of these lands, the B.C. Ministry of Forests provided logistic support, while the National Research Council of Canada awarded funding for the current study, which collected baseline data against which to assess range trend and the success of current and future grazing management programs. Specific objectives were to (1) collect and identify the floral elements of alpine-subalpine communities of the southern Chilcotin Mountains, (2) characterize and map alpine-subalpine vegetation units, and (3) compare grazed and ungrazed sites in terms of botanical composition and community structure. This paper reports only those results associated with plant species collected which represent range extensions for the province of British Columbia.

Study Site

The study area (Fig. 1) is located in the southern Chilcotin Mountains, which lie along the eastern side of the Pacific Ranges physiographic unit of Holland (1976). Relay Valley, also known as the Charlie Cunningham area, lies only 215 km north of Vancouver, British Columbia, at approximately 51°11′N latitude and 123°W longitude. The primary areas of study included Relay Valley, Relay Basin, Two Lakes Basin (Grave-

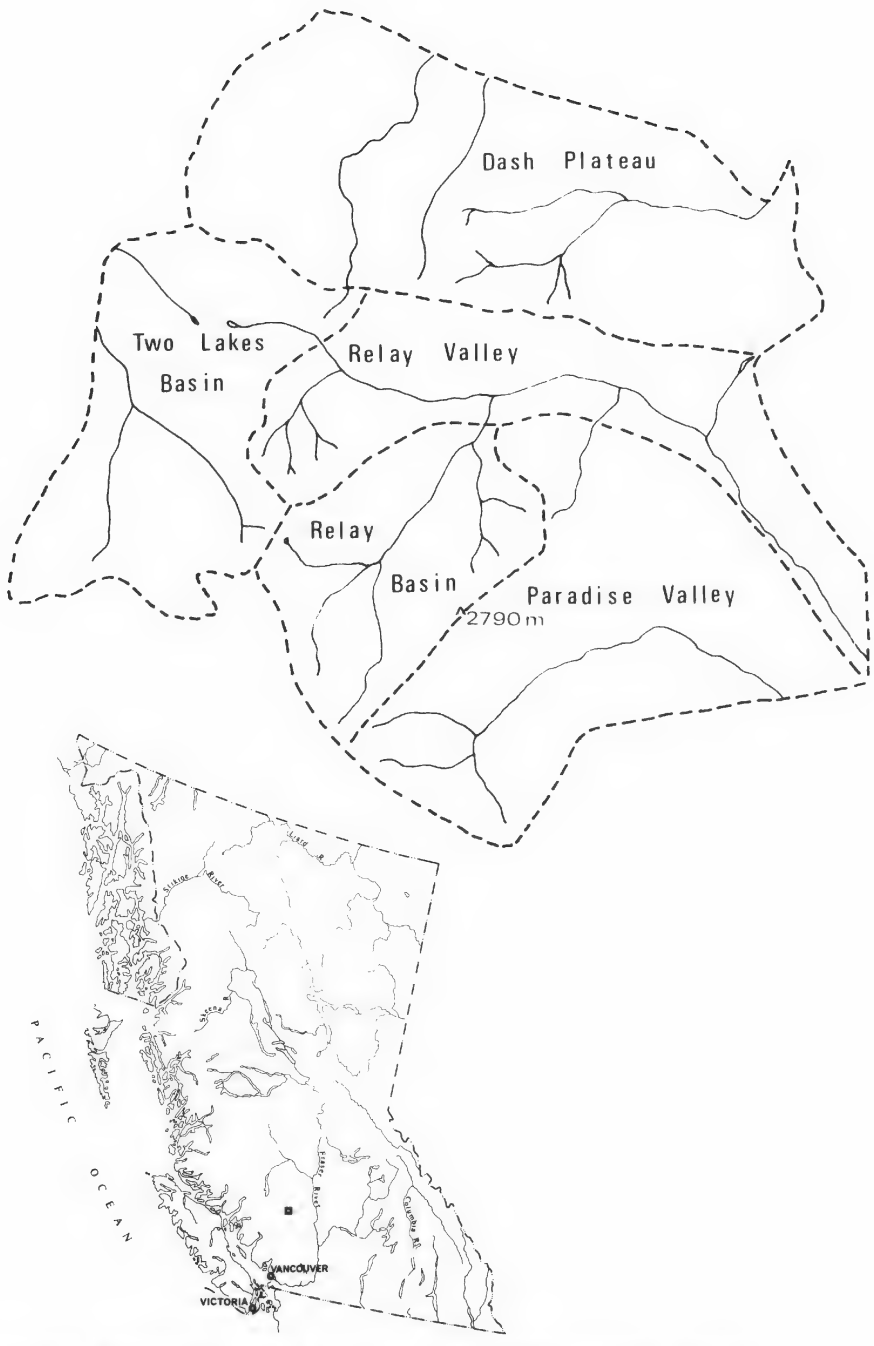


Figure 1. Relative location of the southern Chilcotin Mountains in British Columbia.

yard Valley), and the Dash Plateau, which comprise four grazing units as delineated by the B.C. Forest Service, Range Branch, in Williams Lake (Fig. 1). A small part of the Paradise Valley grazing unit was also sampled, producing a total study area encompassing approximately 100 sq. km (10,000 ha). Relief ranges from 1600 m to 2790 m at the peak of Relay Mountain. Timberline occurs between 2000 m and 2100 m.

Although no glaciers occur in the study area, the effects of Pleistocene glaciation are evident with U-shaped valleys and rounded summits. Soil parent material is primarily of glacial origin, especially in the valleys where Dystric Brunisols have developed on morainal deposits. These are acidic soils possessing relatively thin, poorly decomposed organic surface layers with little incorporation of organic matter in the mineral soil (Valentine *et al.* 1978). At higher elevations, colluvial processes on steep topography have produced unstable areas with little soil development. Regosols predominate, with patterned ground resulting from frost action in Rocklands. In localized depressions with high water table and poor drainage, Rego Gleysols have developed (ELUC, Provisional Map).

The vegetation of the study area lies within two biogeoclimatic zones (Krajina 1965), separated primarily on the basis of climate (Beil *et al.* 1976) The Engelman Spruce-Subalpine Fir Zone occurs at lower elevations and is dominated by *Picea engelmanii* Parry., *Abies lasiocarpa* (Hook.) Nutt., *Pinus albicaulis* Engelm., and *Pinus contorta* Dougl. Shrubby species include *Salix* spp. and *Betula glandulosa* Michx. The Alpine Tundra Zone occurs at higher elevations, above 2000 m, and supports a vegetation dominated by herbs, bryophytes, and lichens, with some low shrubs. Herbaceous meadows are dominated by *Festuca* spp., *Poa* spp., *Carex* spp., plus numerous forbs.

Methods

Two hundred and thirty-nine sites were visited during the summer of 1977. The sampling procedure, adapted from Douglas (1974) and Pojar (1977), permitted a large area to be covered within a limited amount of time. Sample plots were randomly located within homogeneous vegetation units delineated on aerial photographs. Plot size, measured as the radius of a circle, varied in relation to plant physiognomy: herbaceous vegetation, 1 m radius; low shrub, 3 m radius; tall shrub, 7 m radius; forest, 15 m radius. Crown cover was estimated for all species found within these respective plots using the six cover classes identified by Daubenmire (1959): 0-5 percent, 5-25 percent, 25-50 percent, 50-75 percent, 75-95 percent, and 95-100 percent. Rare species, which occurred within the stand but outside the plot, were also recorded. Other parameters recorded for each plot included slope, aspect, elevation, hygrotope, and soil temperature at a depth of 20 cm.

Data were used to describe floristically and environmentally similar plant communities. Tabular analysis utilizing the computer program developed by Ceska and Roemer (1971) identified nineteen plant communities within five major physiognomic types. These results will be reported elsewhere. The following discussion reports only those plant species collected which document range extensions within British Columbia. Hitchcock and Cronquist (1973) and Hultén (1968) served as taxonomic authorities.

Range Extensions

Carex illota Bailey (Cyperaceae). This species was found at only one location, in an

alpine fellfield on Dash Plateau, northwest of the cirque. Elevation 2275 m; gentle slope (6°); N aspect; very rocky, convex xeric site. Associate species: *Salix cascadensis* Cockerell, *Arenaria obtusiloba* (Rydb.) Fern, *Luzula spicata* (L) DC., *Stereocaulon* spp. Hoffm., *Sibbaldia procumbens* L., and *Poa alpina* L.

The range of this plant is described as Olympic Mountains and Cascades, Washington, and adjacent British Columbia, south to Sierran California, east to Montana and Colorado (Hitchcock and Cronquist 1973). This species occurs on wet sites, often above timberline, and in British Columbia has been collected only in Garibaldi Park and Strathcona Park. These two sites are on the southwestern mainland coast and Vancouver Island, respectively. Thus, the current collection represents the first reported observation of *Carex illota* for the interior of British Columbia.

Carex limnophila Hermann (Cyperaceae). This species was collected at three sites, one of which was the Relay Cabin horse pasture, dominated by *Taraxacum officinale* Weber and *Achillea millefolium* L. The remaining two collections occurred in hygric willow-birch wetlands, with *Betula glandulosa* Michx. common to both plots, co-dominated by *Salix barclayi* Anderss. (subalpine) and *Salix barrattiana* Hook. (alpine), respectively. Elevation ranged between 1650 and 1955 m, with a nearly level (0-3°) slope.

Carex limnophila is seldom collected but is described as widespread in wet, montane areas of Mt. Rainier in Washington, the Wallowa Mountains in Oregon, to Alberta and Wyoming south to Nevada and Colorado (Hitchcock and Cronquist 1973). This species has been collected at only two other locations in British Columbia. One collection occurred near Hope, with a second collection northwest of Williams Lake. Therefore, the present investigation documents the existence of individuals which occur between these two earlier, relatively disjunct populations of *Carex limnophila* in British Columbia.

Carex paysonis Cham. (Cyperaceae). This species was collected in a willow-birch shrub wetland on the east side of Dash Plateau. Elevation 2190 m; very gentle slope (4°); N aspect; slight concave hygric site. Cover dominants at this single collection site included *Salix brachycarpa* Nutt., *Betula glandulosa* Michx., and the bryophyte *Drepanocladus aduncus* (Hedw.) Warnst.

Carex paysonsis is uncommon in British Columbia, with previous collections from Mount Rowe in southeastern British Columbia and the Elaho River and Meager Creek in southwestern B.C. Hitchcock and Cronquist (1973) list the range of this species beyond the borders of British Columbia, occurring in southwestern Alberta to western Wyoming and Utah, west across central Idaho to northeastern Oregon and eastern Nevada. Habitats are described as moist meadows to rocky slopes, often above timberline.

Erigeron purpuratus Greene (Compositae). This plant species was found in a rockland community on the peak of Relay Mountain at an elevation of 2790 m. The volcanic parent material supported a xeric vegetative community dominated by the lichens *Rhizocarpon geographicum* (L.) DC. and *Umbilicaria* spp. Hoff. Although rare in British Columbia, *Erigeron purpuratus* has been collected both in the northern (Spatsizi) and in the southern portions (Tchaikazan Valley, Glacier Park, and Invermere) of the Province. Prior to the current discovery, the southern collections were identified as *Erigeron pallens* Cronq. Detailed work by Douglas and Ceska (in press), however, concludes *E. pallens* to be synonomous with *E. purpuratus*, which is com-

monly found in the Yukon and Alaska. Hitchcock and Cronquist (1973) describe the range of *E. pallens* as Rocky Mountains to California north to the Wallowa Mountains.

Eriophorum brachyantherum Trautv. and Mey. (Cyperaceae). This circumboreal species is common throughout northern British Columbia and occurs in the Rocky Mountains of southeastern British Columbia (Hultén 1968). Although not reported previously in the southwestern portion of the province, this species occurred commonly in the *Salix barrattiana* Hook. shrub wetland of Two Lakes Basin. *Betula glandulosa* Michx. co-dominated this single collection site, located at 1955 m with 8° south-facing slope.

Gentiana prostrata Haenke (Gentianaceae). Previous collections of this species have all occurred in the northern part of the province, although both Hitchcock and Cronquist (1973) and Hultén (1968) indicate that it occurs in South America, presumably in similar habitats of alpine bogs and high, montane meadows. The current investigation found *G. prostrata* only in a birch-willow community at 1955 m on a south-facing, gentle slope of Two Lakes Basin. Dominant associates included *Salix brachycarpa* Nutt. and *Betula glandulosa* Michx. The hummocky, hygric site supported occasional *Pinus contorta* Dougl. to a height of 6.5 m.

Papaver lapponicum (Tolm.) Nordh. subsp. *occidentale* (Lundstr.) Knaben. A rare species in British Columbia, this plant has been collected previously in the Hazelton Mountains in the northwestern part of the Province and on Mount Assiniboine in the Rocky Mountains. The current discovery on the eastern edge of Dash Plateau represents a significant range extension in British Columbia. This species was found in an alpine tundra on a north-facing ridge at 2220 m. The steep (25°), rocky, xeric site was dominated by *Cetraria nivalis* (L.) and *C. islandica* (L.) Ach., with *Kobresia myosuroides* (Vill.) Fiori also present.

Papaver lapponicum subsp. *occidentale* is a complex described by Kartesz and Kartesz (1980) as synonymous with *P. radicatum* Rott. and *P. kluanensis* D. Love. Moss (1974) describes *P. kluanensis* as existing on exposed alpine sites of the Rocky Mountains in southwestern Alberta, but neither Hitchcock and Cronquist (1973) nor Hultén (1968) included *P. radicatum* or *P. kluanensis* in their respective floras.

Ranunculus gelidus Kap. & Ker. (Ranunculaceae). This plant species was found on the same plot as *Erigeron purpuratus*, in a rockland community, dominated by crustose lichens on the peak of Relay Mountain. Although rare in the Province, *Ranunculus gelidus* has been collected previously in northern British Columbia (Mt. Edziza and on the Spatsizi Plateau) and in the Rocky Mountains. Hitchcock and Cronquist (1973) describe the range as Alaska and northern Canada, south on talus slopes and alpine meadows to British Columbia, Alberta, Montana, and Colorado. The current collection represents a significant southward range extension for British Columbia.

Ranunculus inamoenus Greene (Ranunculaceae). This plant has been identified only rarely in British Columbia, with the previous collections representing a disjunct distribution. Two of these earlier collections, from the Flathead and Wall Lake Regions in southeastern British Columbia, are within the species range described by Hitchcock and Cronquist (1973). Other collections, however, lie considerably beyond this range, approximately 400 km northwest of the study area at Anzus Lake and in the Ilgachuz Mountains. The presence of *R. inamoenus* in Graveyard Valley links these two disjunct populations together and suggests that this species may be more common in

British Columbia than existing botanical references indicate. Associate species in Graveyard Valley are typical of a sub-xeric, fescue meadow community and include *Festuca brachyphylla* Schult., *Cerastium arvense* L., and *Geum triflorum* Pursh. Past grazing use by cattle was evident in most stands sampled.

Cinclidium stygium Sw. (Mniaceae). Lawton (1971) summarizes a circumboreal distribution for this species, although Schofield (pers. comm.) believes this collection to be the first Provincial identification for *C. stygium* south of Prince George, British Columbia. Its single occurrence in a high elevation (1940 m), *Carex rostrata* Stokes sedge wetland on the valley floor of Two Lakes Basin is consistent with its preferred habitat of wet places and arctic bogs.

Discussion

Disjunct populations are those separated geographically from the major distribution centers for the respective plant species (Meinke 1980). Of the ten plant species presented thus far, all fall into this disjunct category. The collection of *Papaver lapponicum* subsp. *occidentale* represents a considerable disjunction of 600 and 350 km from the two previous collections in northwestern and southeastern British Columbia, respectively. Four other plant species—*Erigeron purpuratus, Ranunculus gelidus, R. inamoenus,* and *Cinclidium stygium*—display disjunct distributions ranging from 350 to 450 km, whereas *Carex illota, C. limnophila, C. paysonis, Eriophorum brachyantherum,* and *Gentiana prostrata* all extend 120 to 200 km beyond previous collections.

The peak of Relay Mountain, at 2790 m, remained exposed during the most recent period of glaciation in British Columbia and thus may have provided a refuge for some species which now have disjunct populations. *Erigeron purpuratus* and *Ranunculus gelidus*, which were observed in the current study only as a few, scattered individuals on Relay Peak are two of the plant species with range extensions exceeding 400 km beyond previous collections. *Poa lettermanii* Vasey is a common species on higher peaks in the Rocky Mountains and southwestern British Columbia. Like *Erigeron purpuratus* and *Ranunculus gelidus*, however, *Poa lettermanii* also occurred only as isolated individuals on Relay Peak, lending additional support to the proposition that these disjunct populations in British Columbia may have survived in refugia during Pleistocene glaciation.

Range Limits

Five species collected within the study area appear to be at or near the limits of their ranges. *Haplopappus lyallii* Gray, found growing sporadically on the scree slopes of Relay Mountain, is described by Hitchcock and Cronquist (1973) as occurring in British Columbia and Alberta to Washington, northeastern Oregon, northeastern Nevada, and Colorado. The authors are not aware of any other collections of *Haplopappus lyallii* north of the study area.

Three additional species may also be growing at the northern limit of their distributions in Relay Valley. *Senecio elmeri* Piper occurs commonly at high elevations in Washington and southern British Columbia and was found as scattered pockets of abundant individuals on the rocky slopes of Relay Mountain and nearby ridges. *Salix cascadensis* Cockerell, a common species in southeastern British Columbia and the Washington Cascades, grew abundantly on Dash Plateau, a gently sloping, sub-mesic habitat conducive to this northernmost population of *S. cascadensis*.

Lupinus lepidus Dougl. var. *lobbii* (Gray) Hitchc. is extremely common south of British Columbia but occurs sparingly within the province. Based upon empirical observations, *Lupinus lepidus* var. *lobbii* apparently grows at its northern limit in Two Lakes Basin. Although this species is considered a community dominant in some alpine areas of Washington (Del Moral 1979), only a single, albeit dominant, stand of *Lupinus lepidus* var. *lobbii* was observed in the current study.

Festuca altaica Trin. occurs commonly in northern British Columbia, the Yukon, and Alaska. Although widespread in the southern Chilcotin Mountains, this species has not been reported south of the current study site, where *F. altaica* apparently reaches the southern limits of its distribution.

Although *Populus trichocarpa* T. and G. occurs abundantly at low elevations throughout British Columbia west of the Rocky Mountains, it is seldom found at high elevations. The only previous high elevation collections of *P. trichocarpa* in the University of British Columbia herbarium are from Garibaldi Park in southwestern British Columbia, at 1520 m. The current investigation, however, discovered specimens only 15 cm tall growing at an elevation of 2190 m in Relay Valley, suggesting that *Populus trichocarpa* has a wide ecological amplitude.

Rare and Endangered Species

Three plants identified in the current study are listed by Taylor and MacBryde (1977) as rare in British Columbia: *Ranunculus gelidus, Lupinus lepidus,* and *Papaver lapponicum* subsp. *occidentale.* A workshop in 1978 (Taylor, unpub. ms.) reviewed the concept of rare and endangered plant taxa in British Columbia, and produced the following categories for degree of rarity: R1—single or few populations; R2—several populations, locally common; R3—widespread or scattered distribution; R4—restricted distribution, large populations. *Papaver lapponicum* subsp. *occidentale* was not included on the preliminary list of plants belonging to these categories, perhaps because of the confounding taxonomic synonomy associated with this species. *Ranunculus gelidus* displays a scattered distribution (R3) and is therefore not an endangered plant species within British Columbia, although only two individual plants were observed throughout the entire study area during the summer of 1977.

Presumably R1, single or few populations, would describe those plants most endangered or susceptible to provincial extinction. Of the three species deemed to be rare, only *Lupinus lepidus* falls into this category. Interestingly, *Erigeron purpuratus* is also assigned to this R1 category, although its status in Taylor and MacBryde (1977) is listed as "not endangered." These apparent anomalies likely reflect the relative isolation of the single or few populations of both *Lupinus lepidus* and *Erigeron purpuratus.*

Meinke (1980) discussed the need for identifying rare and endangered plant species on an individual population basis, irrespective of whether the species is rare within the state or geographical region. Moreover, the criteria used for evaluating additions to the rare and endangered list should be expanded to include disjunct populations which may provide important genetic variability even at the recognized species level. This perception is particularly relevant to British Columbia, a geographically vast region which likely harbors many disjunct populations on mountain peaks that escaped recent glaciation. The current investigation has identified several plant species which represent such disjunct populations. Although the Relay Valley area may be deemed

to represent a transition between boreal and temperate flora, as well as coastal and continental flora, the disjunct populations discovered at this location are not believed to be unique or isolated occurrences. Future botanical investigations, particularly in the northern portions of British Columbia, will almost certainly add to the list of genetically isolated plant populations at the species level.

Literature Cited

Beil, C. E., R. L. Taylor, and G. A. Guppy. 1976. The biogeoclimatic zones of British Columbia. Davidsonia 7(4):45-55.

Ceska, A., and H. Roemer. 1971. A computer program for identifying species-releve groups in vegetation studies. Vegetatio 23(3-4):255-277.

Daubenmire, R. 1959. A canopy coverage method for vegetation analysis. Northw. Sci. 33(1): 43-64.

Del Moral, R. 1979. High elevation vegetation of the Enchantment Lakes Basin, Washington. Can. J. Bot. 57(10):1111-1130.

Douglas, G. W. 1974. Montane zone vegetation of the Alsek River region, southwestern Yukon. Can. J. Bot. 52:2505-2532.

———, and O. Ceska. The taxonomic status of *Erigeron purpuratus* and *Erigeron pallens* (Asteraceae). In press. Systematic Botany.

Environment and Land Use Committee. Provisional Map. Assessment and Planning Division, Catalogue 81, B.C. Ministry of Environment, Soil and Landform Map 920 (2/3), 1:50,000.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest: An illustrated manual. Univ. of Wash. Press, Seattle.

Holland, S. S. 1976. Landforms of British Columbia: A Physiographic Outline. Bull 48, British Columbia Department of Mines and Petroleum Resources.

Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford Univ. Press, Stanford, California.

Kartesz, J. T., and R. Kartesz. 1980. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland. Vol. II. The Biota of North America, Univ. of North Carolina Press.

Krajina, V. J. 1965. Biogeoclimatic zones and classification of British Columbia. Ecol. West. N. Amer. 1:1-17.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Nichinan, Miyazaki, Japan, Hattori Botanical Laboratory.

Meinke, R. J. 1980. Some range extensions and a new state record for the Oregon flora. Northw. Sci. 54(4):237-243.

Moss, E. H. 1974. Flora of Alberta. Univ. of Toronto Press, Toronto and Buffalo.

Pojar, J. 1977. Vegetation and Some Plant-Animal Relationships of Ecological Reserve #68, Gladys Lake. Unpublished Report of Ecological Reserves Unit, Land Management Branch, Department of Environment, Victoria, British Columbia.

Schofield, W. B. 1981. Pers. Comm. Professor, Dept. of Botany, Univ. of British Columbia.

Selby, C. J. 1980. Alpine and Subalpine Vegetation in the Southern Chilcotin Mountain Rangelands of British Columbia. M.Sc. Thesis. Dept. Plant Sci., Univ. British Columbia.

Taylor, R. L. Unpublished Manuscript. Preliminary List of the Rare Plants of British Columbia, Botanical Gardens, Univ. British Columbia.

———, and B. McBryde. 1977. Vascular Plants of British Columbia Tech. Bull #4. Botanical Gardens, Univ. of British Columbia Press.

Valentine, K. W. G., P. N. Sprout, T. E. Baker, and L. M. Lavkulich. 1978. The Soil Landscapes of British Columbia. Resource Analysis Branch, Ministry of the Environment, Victoria, British Columbia.

Received June 1, 1981
Accepted for publication October 2, 1981

S. J. Wikeem

Agriculture Canada Research Station
3015 Ord Road
Kamloops, British Columbia V2B 8A9

and

Michael D. Pitt

Department of Plant Science
University of British Columbia
Vancouver, British Columbia V6T 2A2

Soil Nitrogen Gradients as Influenced by Sagebrush Canopy in Southern British Columbia[1]

Abstract

A sagebrush (*Artemisia tridentata*) community was investigated in the southern interior of British Columbia to determine the existence of horizontal gradients in soil nutrients as a function of the shrub canopy layer. Higher concentrations of total soil nitrogen were present in soil beneath the shrub canopy (1747 ppm) as opposed to the interspace zone (1493 ppm). Ammonium nitrogen was also more prevalent at the canopy site (82.0 ppm) compared to interspace soils (67.4 ppm), while nitrate nitrogen reversed this trend, with significantly greater concentration in interspace soils (8.1 ppm) than beneath the canopy layer (3.3 ppm). Foliar nitrogen concentration of bluebunch wheatgrass (*Agropyron spicatum*) did not differ significantly between these two sites.

Averaged over both canopy and interspace locations, total soil nitrogen increased from 1525 ppm in May to 1715 ppm in August. Soil ammonium nitrogen declined from 84.6 ppm to 65.0 pm during this same period, while soil nitrate nitrogen remained unchanged. These phenomena were discussed in terms of the competitive relationship among native and introduced (*Bromus tectorum*) plant species of the sagebrush community.

Introduction

Vertical soil nutrient gradients, where highest concentrations are found on the surface, occur with most vegetation types as a result of litter deposition. Horizontal gradients, however, are limited to vegetation types which do not form a continuous canopy. Such patterned vegetation is characteristic of arid and semiarid shrublands. Because of their far-reaching root systems, which extend both laterally and vertically, dryland shrubs are able to draw nutrients from a large area. Litter deposition, though, is restricted to the area directly under the canopy. Thus, with successive depositions over time, organic matter, and the nutrients contained within it, accumulate under the shrub's canopy at the expense of the interspace soils.

This horizontal, anisotrophic effect has been demonstrated for sodium, potassium (Rickard and Keough 1968), organic carbon, organic phosphorus (Charley and West 1975), total sulfur (Tiedemann and Klemmedson 1973a), and nitrogen (Garcia-Moya and McKell 1970, Rixon 1971, Tiedemann and Klemmedson 1973a, Charley and West 1975). Of these parameters, nitrogen is the nutrient most likely to limit plant production on arid rangelands (Charley 1977).

[1]This research was supported in part by the National Science and Engineering Research Council of Canada, Project #67-0227. The senior author conducted this research as partial fulfillment of the requirements for a B.Sc. degree in Agricultural Sciences at the University of British Columbia, 1979.

In the Mojave Desert, the canopy soils of catclaw acacia (*Acacia gregii*), desert senna (*Cassia armata*), and creosote bush (*Larrea divaricata*) all demonstrated higher nitrogen concentration than the open, non-covered soils (Garcia-Moya and McKell 1970). This patterning of nitrogen around shrubs was attributed to unequal litter deposition, the shrub's protective role against wind erosion, and the favourable understory microclimate for grasses and forbs.

In Utah, shrub-induced anisotrophy was investigated for the dominant species of several vegetation types (Charley and West 1975). Shadscale (*Atriplex confertifolia*), big sagebrush (*Artemisia tridentata*), and blackbush (*Coleogyne ramosissima*) all showed nitrogen concentation differentials, although there were intercommunity differences in the degree of patterning expressed. These differences, which existed both among species and within the same species at different sites, were thought to reflect differences in maturity of shrubs, chemical and physical irregularity of soil parent material, or surface disturbance. There was no consistent relationship between degree of enrichment and aridity of climate.

Although nitrogen redistribution has been well documented, most studies have not determined if under-canopy accumulation results in greater nitrogen availability or enhanced growth for understory plants. Rixon (1971) compared nitrification in soils collected from interspace and saltbush (*Altriplex vesicaria*) dominated soils and found increases in both initial nitrate and total nitrogen and a higher rate of nitrate production in the shrub affected soils. Interestingly, the difference in nitrate production between the open and canopy sites was greater than these respective differences in soil total nitrogen. Rixon hypothesized that organic residues from saltbush may have higher nitrification rates than those residues derived from plants of the interspace area. Mineralization studies of sagebrush associated soils support this hypothesis, with production of mineralized ammonium and nitrate in higher quantities than can be explained by total nitrogen concentrations alone (Charley and West 1977).

Tiedemann and Klemmedson (1973b) hypothesized that the greater abundance of perennial grasses observed under mesquite (*Prosopis juliflora*) may be accounted for partially by increased availability of such mineralized nutrients. In their work, relative availability of nutrients was determined by calculating relative yields of three perennial grasses grown in soils collected from beneath canopy and adjacent locations. Greatest relative yield was observed for plants harvested from mesquite influenced soil, with nitrogen, sulphur, and phosphorus all more relatively available. Strikingly, relative availability of nitrogen was up to 15 times higher in mesquite soils, even though total nitrogen was only three times greater.

Rickard *et al.* (1973) found similar results for the annual plant cheatgrass (*Bromus tectorum*) growing in soils collected from interspace areas and beneath the canopies of greasewood (*Sarcobatus vermiculatus*) and hopsage (*Grayia spinosa*), as cheatgrass biomass increased 100 percent on soils associated with a shrubby overstory. Moreover, the average percent nitrogen of cheatgrass foliage was directly influenced by canopy soils, averaging 6.1, 4.2, and 2.7 percent on greasewood, hopsage, and interspace soils, respectively.

In the Pacific Northwest, sagebrush canopies also produce an apparent benefit to understory, herbaceous vegetation. Daubenmire (1975) remarked that cheatgrass growing beneath sagebrush frequently forms a conspicuous, dense stand that coincides with

the area of the canopy above. He attributed this phenomenon to the accumulation of litter and grasshopper frass below the shrub which provides a thick and fertile bed for cheatgrass caryopses. Similarly, Kline and McKell (1974) found a four-fold biomass increase of cheatgrass and Japanese bromegrass (*Bromus japonicus*) beneath the overstory of sagebrush. Chemical analyses of these grasses demonstrated that the increased growth probably resulted from an improved nitrogen supply (Charley 1977).

No published research investigating shrub-induced nitrogen concentration gradients is available for British Columbia. Previous studies in the Pacific Northwest have always evaluated more southerly and more xeric range plant communities. Possibly, with the more mesic conditions of interior British Columbia, soil nitrogen redistribution would be less pronounced than those present in Palouse Prairie shrublands.

Although considerable effort has been directed to evaluating competition between sagebrush and bluebunch wheatgrass (*Agropyron spicatum*) in British Columbia, the potential relationship between shrub-induced anisotrophy and resultant competitive advantage over this important climax, forage grass has not been considered. Therefore, the objectives of this study were to: (1) determine if sagebrush communities of interior British Columbia caused patterns of soil nitrogen accumulation and depletion; (2) determine shrub induced differences in available ammonium and nitrate; (3) determine if nitrogen content of bluebunch wheatgrass differed between the canopy and interspace microhabitats; and (4) determine if anisotrophic factors were influenced by seasonal progression.

Study Area

The study area is located near Kaleden, British Columbia, on the east side of the Okanagan Valley (49°26′N, 119°37′W). Although valley sides are steep, the study site occurs on a terrace with a gentle slope (10 percent), at an elevation of 670 m, and a north-east exposure. Soils are shallow, with gravelly, silty-loam texture.

The climate is continental with cold winters (January mean –3° C), hot summers (July mean 20° C), and approximately 150 frost-free days. The mean annual precipitation equals 29.6 cm, with bimodal peaks in January (3.1 cm) and June (3.6 cm) (Environment Canada 1974).

Big sagebrush dominated the study site, in terms of both botanical composition (17.3 percent) and cover (17.5 percent). Other important botanical components (nomenclature by Hitchcock and Cronquist 1973) included Sandberg's bluegrass (*Poa secunda*), 13.3 percent; cheatgrass, 10.7 percent; needleandthread (*Stipa comata*), 8.6 percent; bluebunch wheatgrass, 8.6 percent; and six-weeks fescue (*Festuca octoflora*), 5.0 percent. Blue-eyed Mary (*Collinsia parviflora*) was the most abundant forb at 10.7 percent botanical composition, while balsamroot (*Balsamorhiza sagittata*) equaled 7.8 percent. Grey rabbitbrush (*Chrysothamnus nauseosus*), 1.3 percent, was the only shrub present other than big sagebrush. *Selaginella wallacei* was an important component of the vegetation, contributing 11.8 percent of the botanical composition. Total plant cover on the study site equaled 80 percent and 62 percent in May and August, respectively.

Soil pH equaled 6.4 at both the shrub and interspace locations, while bulk density averaged 1.24 g/cm^3 and 1.35 g/cm^3 in the canopy and interspace soils, respectively.

Sampling Procedure

Sampling began on 16 May 1978 and was repeated on 22 August 1978. May, a cool moist month, was assumed to produce favourable conditions for mineralization, particularly in comparison to August when soils are hot and dry. Sampling for soils and vegetation occurred simultaneously on 20 shrub-dominated sites and 20 interspace sites. These 20 samples were combined for soils and vegetation, respectively, to produce a composite sample for the shrub and interspace sites.

Canopy soils were collected only from beneath shrubs with dense, well-developed canopies. Soil core samples to a depth of 15 cm, including surface litter, were removed from locations approximately half-way between the crown and canopy edge. Samples were not collected from beneath the aerial projections of grasses or forbs, which may have confounded the influence of sagebrush. To avoid possible effects of downslope leaching, soil cores were always removed from the contour side of the shrub. All interspace samples were then collected from an associated area with no shrubs present for a one-meter radius.

The soil was placed in plastic bags and frozen immediately. After returning to Vancouver, the soils were air-dried, ground to 2 mm particle size, and stored in plastic bags until required for analysis.

At each shrub canopy soil sampling location, understory bluebunch wheatgrass plants were clipped to a 15 cm height. Forage samples from the interspace sites were collected from bluebunch wheatgrass plants near the soil core location but still in the interspace zone. Plants of approximately the same size were used for all forage samples which retained the new growth of leaves only. Oven-dried samples (70°C) were then ground with a 40 mesh Wiley Mill and stored in glass bottles for future analyses.

Laboratory Analysis

Nitrogen concentration of bluebunch wheatgrass was determined from five replicates of the composited oven-dried material from canopy and interspace sites, respectively, by the Macrokjeldahl method.

Soil total nitrogen was determined using Bremner's (1965) regular Macrokjeldahl method with the following modifications. Rather than digesting the sample under gentle heat for 5 hours, sulfuric acid was added to the sample and left to digest at room temperature overnight. Catalysts were then added and the mixture was heated for 1.5 hours after the digest had cleared. Bumping during the distillation was prevented by using a sand-free aliquot of the digest. Exchangeable ammonium was determined by Nesslerization after the soil had been extracted with acidified NaCl, while nitrate nitrogen was evaluated with the Phenol disulphuric acid method (Jackson 1958). These soil parameters were all determined with five replicates, while the statistical effects of shrub canopy and month of sampling on total N, ammonium, nitrates, and forage N were analyzed with a two-way analysis of variance ($\alpha = .05$).

Results

Mean values for total nitrogen, exchangeable ammonium nitrogen, and nitrate nitrogen concentrations (ppm) are presented in Table 1. The values in parentheses represent an extrapolation to kilograms per hectare from parts per million to give an approximation

TABLE 1. Total nitrogen (N) concentration, exchangeable ammonium nitrogen (NH_4^+ N) concentration, and nitrate nitrogen (NO_3^- N) concentration for canopy and interspace soils in May and August.

Treatment		N ppm	N (Kg/ha)	NH_4^+ N ppm	NH_4^+ N (Kg/ha)	NO_3^- N ppm	NO_3^- N (Kg/ha)
Month	May	1525	(2162)	84.6	(120.0)	5.5	(7.8)
(n=10)	August	1715	(2432)	65.0	(92.1)	5.9	(8.4)
			*		*		NS
Location	Canopy	1747	(2477)	82.0	(116.3)	3.3	(4.7)
(n=10)	Interspace	1493	(2117)	67.4	(95.6)	8.1	(11.5)
			*		*		*
Month	May Canopy	1658	(2351)	94.0	(133.3)	3.2	(4.5)
X	May Interspace	1392	(1974)	75.1	(106.5)	7.8	(11.0)
Location	August Canopy	1836	(2603)	70.1	(99.4)	3.3	(4.7)
(n=5)	August Interspace	1594	(2260)	59.8	(84.8)	8.5	(12.0)
			NS		NS		NS

* Treatment means differ at the 0.05% level of significance.

NS Treatment means do not differ at the 0.05% level of significance.

of these soil parameters on a field scale. Soil total nitrogen was significantly greater under the sagebrush canopy (1747 ppm) than in the interspace soils (1493 ppm). Canopy and interspace soils, respectively, both produced higher total nitrogen in August (1836 ppm; 1594 ppm) than in May (1658 ppm; 1392 ppm), although the magnitude of these differences was not significantly influenced by the interaction with soil location (Table 1).

Soil location and sampling month also significantly influenced exchangeable ammonium nitrogen, but as with total nitrogen there was no statistical interaction (Table 1). Ammonium nitrogen in soil samples from beneath the shrub canopy averaged 82.0 ppm, compared to 67.4 ppm for the interspace soils, with total ammonium nitrogen concentration declining from 84.6 ppm in May to 65.0 ppm in August.

Concentrations of nitrate nitrogen significantly differed between canopy and interspace soils but were not significantly affected by month of sampling (Table 1). For both May and August, the concentration of nitrates of the interspace soils more than doubled that of the canopy location. Interspace soils averaged 7.8 ppm and 8.5 ppm in May and August, respectively, while canopy soils in these same two months equaled only 3.2 and 3.3 ppm, respectively.

Table 2 summarizes the results for forage quality analyses, which indicate that nitrogen concentration in bluebunch wheatgrass declined from May to August but was not significantly influenced by soil location. In May, the mean nitrogen concentration of bluebunch wheatgrass equaled 1.88 percent, more than double the 0.76 percent present in August. Nitrogen concentration in the foliage of canopy and interspace plants averaged 1.31 and 1.33 percent, respectively.

Discussion

Although higher concentrations of total soil nitrogen and ammonium nitrogen were found in soils beneath sagebrush canopy, much higher concentrations of nitrate nitrogen were found in the interspace soils. This apparent quandary is best explained by first investigating the major steps in the nitrogen cycle with reference to the current study.

Following litter deposition, the initial step of mineralization is proteolysis, occurring

TABLE 2. Percent nitrogen concentration (Forage N) of bluebunch wheatgrass plants inhabiting canopy and interspace sites in May and August.

		Percent Forage N (Crude Protein)[1]	
Month (n=10)	May	1.88	(11.75)
	August	0.76	(4.75)
		*	
Location (n=10)	Canopy	1.31	(8.19)
	Interspace	1.33	(8.31)
		NS	
Month X Location (n=5)	May Canopy	1.88	(11.75)
	May Interspace	1.89	(11.81)
	August Canopy	0.74	(4.64)
	August Interspace	0.78	(4.88)
		NS	

[1] Crude protein equals percent forage N x 6.25.

* Treatment means differ at the 0.05% level of significance.

NS Treatment means do not differ at the 0.05% level of significance.

when the litter proteins are broken apart to form amines and amino acids. In this study, soil total nitrogen increased from May to August, by which time most plant production had ceased for the year, with large quantities of plant material returned to the soil as litter. Consequently, total soil nitrogen was higher in August than in May. Sagebrush, although retaining its leaves year-round, is semi-deciduous and sheds its large summer leaves during the summer drought period (Daubenmire 1975). Because of increased quantities of litter beneath these shrubs, total soil nitrogen was subsequently higher in the undercanopy soils than in the interspace soils, lending support to similar results of Charley and West (1975).

Sagebrush tends to be a successful accumulator of undercanopy soil nitrogen because of two primary attributes. First, this plant species retains its litter well, as the small, dense leaves fall directly beneath the canopy. Frequently, decaying sagebrush leaves define a silvery boundary line on the soil at the canopy's edge. Except on downslope positions, this line extends little more than a few centimeters from the canopy boundary. Secondly, the root system of sagebrush is well suited for drawing nitrogen from an area larger than its crown cover with a deep tap root plus an extensive system of lateral roots near the soil surface. Although these lateral roots can extend far beyond the axis of the plant (Daubenmire 1975), most are concentrated under the canopy (Tabler 1964). This combination of tap and lateral roots allows sagebrush to utilize both surface and subsurface moisture and nutrients.

After proteolysis has occurred, the next major process is ammonification. Heterotrophic organisms utilize the amines and amino acids released from proteolysis and change them to ammonia. Ammonia is readily converted to ammonium, which is then subject to one of the following fates: (1) it may be absorbed by higher plants; (2) ammonium ions may be adsorbed tightly to the inter-lattice spaces of clay minerals or held less tightly on the exchange complex of the soil colloids; (3) nitrogen may be lost through volatilization of ammonia; or (4) autotrophs may oxidize ammonium to nitrites and nitrates.

In contrast to total nitrogen, exchangeable ammonium nitrogen declined from May to August. Presumably, much of the ammonium present in May had been either

utilized by the plants or lost through volatilization. The addition of total N through litter deposition may have been expected to result in higher ammonium nitrogen concentrations in August. The observed reduction in August concentrations probably reflects the time lag between litter decomposition, proteolysis, and the completion of ammonification. This lag may have resulted from hot, dry soil conditions, which can greatly suppress soil microbial activity. The August samples were collected shortly after a long, hot, dry spell, possibly before soil microbes had resumed ammonification. Weather conditions for the end of August and most of September remained warm but moist. If the soil had been sampled several weeks after the August sampling date, a higher exchangeable ammonium nitrogen concentration may have been observed.

Concentrations of total soil nitrogen and exchangeable ammonium nitrogen were both higher beneath sagebrush canopies than in interspace soils. Although organic carbon was not measured in this study, the sagebrush canopy likely provides increased organic carbon relative to the interspace zones. Total soil nitrogen is primarily organic in nature, while organic carbon serves as the substrate for ammonifying bacteria.

In some studies, large site differentials in mineralization rates have been measured which cannot be explained by total soil nitrogen differentials alone (Rixon 1971, Charley and West 1977). Readily decomposed litter and amelioration of microclimate by the shrub were suggested as explanations for increased mineralization rates. In the present study, the site differential between canopy and interspace soils for total N and exchangeable ammonium were very similar, 1.17 and 1.22, respectively. Nonetheless, microclimate modification and ease of litter decomposition may still have contributed to the observed difference in ammonium concentration between the canopy and interspace sites.

Nitrification, the next major step in mineralization, occurs in two stages. Initially, Nitrosomonas and lesser soil organisms oxidize ammonium to nitrite. Secondly, *Nitrobacter*, another autotrophic bacterium, oxidizes nitrites to nitrates, which are readily available for uptake by plant roots.

Concentrations of soil nitrate nitrogen as influenced by season and location proved to be puzzling in the current study. Unlike total soil nitrogen and ammonium, no difference existed between May and August.

Soil nitrate concentrations were expected to decline during these summer months in response to anticipated slowing of the mineralization rate. Indeed, early August produced very hot weather, with daily temperatures exceeding 35°C. Such conditions would likely suppress nitrification. However, approximately one week prior to the 22 August sampling date, temperatures, although still warm, dropped to daily highs of 24-25°C, with daily rain showers. Perhaps these environmental conditions were more favorable for nitrification, with a resultant increase in nitrates relative to the expected concentrations.

The most thought-provoking discrepancy in the nitrate nitrogen results is the high concentrations of nitrates in the interspace relative to the canopy soils. Several possible explanations exist for this phenomenon. First, sagebrush plants may have utilized the nitrates present in canopy soils. This explanation would appear more probable if the site differential appeared only in August when little else but sagebrush was actively translocating. However, herbaceous ground cover in the interspaces was high in May. These actively growing plants should be utilizing available nitrates, thereby mitigating against increased concentrations in the interspace soils in May. Consequently, differ-

ential use of nitrates by sagebrush probably did not produce the nitrate concentration differential between canopy and interspace soils.

A second possibility is that a lag phase may have occurred between ammonification and nitrification, so that ammonium became unavailable to the nitrifiers. For example, Blackburn and Skau (1974) found that higher infiltration rates of canopy soils led to increased moisture availability. Such favorable conditions subsequently allowed the microbial populations to flourish and thus tie up ammonium through their metabolic activities.

In addition to altered microclimatic conditions, the difference in nitrate nitrogen concentrations between canopy and interspace soils may be explained by the nitrification inhibitory effect of sagebrush litter (Fulgham *et al.* 1975). Neale (1969) demonstrated inhibition by root extracts for several rangeland plants and suggested that the presence of antibacterial substances may be an important mechanism for conserving low quantities of available nitrogen. One of these available forms, ammonium, is absorbed on the cation exchange complex, where it is relatively safe from denitrification or volatilization losses. Interestingly, ammonium volatilization losses appear greatest between shrub canopies (Charley 1977), perhaps reflecting differences in cation exchange capacity between canopy and interspace sites.

The other form of nitrogen commonly used by plants is the anion, nitrate, which is not held on the exchange complex. Consequently, nitrate is subject to losses through denitrification or leaching. Inhibition of nitrification retains soil nitrogen in the more stable ammonium form, which is consistent with the observed results of increased NH_4^+ beneath the sagebrush canopy.

This inhibition theory superficially appears to disagree with Charley and West (1977), who showed higher rates of mineralization in sagebrush canopy soils. However, these researchers combined the total production of ammonium and nitrates to determine mineralization rates. Inhibition of nitrification may therefore have been masked by production of large quantities of ammonium.

For nitrification inhibition to benefit sagebrush, the shrub must necessarily be able to utilize the ammonium form of nitrogen for its nutrition. Wallace *et al.* (1978), working with greenhouse experiments, discovered that when ammonium and nitrates were supplied separately to sagebrush, the shrubs utilized more ammonium than nitrate. Moreover, when the plants were provided a solution of ammonium nitrate that contained equal quantities of each nitrogen form, the uptake ratio of ammonium to nitrate did not change relative to when the plants were supplied these nutrients separately. Over a 72 hour period, sagebrush utilized nearly five times as much ammonium as nitrate, suggesting that nitrification inhibition may indeed benefit sagebrush in its natural environment.

Nitrogen in the Plant: Immobilization

The last stage in the nitrogen cycle is immobilization, occurring when the available forms of nitrogen are taken up by the plants for conversion to organic compounds. In this study, the foliage nitrogen content of bluebunch wheatgrass was measured to reflect immobilization of nitrogen on canopy and interspace sites (Table 2). As documented by many previous studies, foliar nitrogen was significantly higher in May than in August, the end of the growing season. Surprisingly, however, there was no sig-

nificant difference in foliar nitrogen content of bluebunch wheatgrass on canopy and interspace soils. With canopy soils offering more ammonium and the interspace soils offering more nitrate, one of the sites probably should have shown a significantly higher nitrogen content in bluebunch wheatgrass.

As moisture is the factor most commonly limiting plant production in semiarid rangelands, bluebunch wheatgrass may have been unable to benefit from nitrogen enrichment at either of the sites if moisture were unusually limiting. This argument does not convincingly explain the current results, however, as the spring was very moist, as evidenced by the prolific growth of annual species, particularly for six-weeks fescue and Blue-eyed Mary.

Alternatively, bluebunch wheatgrass may not even respond to soil nitrogen enrichment. Mason and Miltimore (1959) conducted a series of fertility trials on bluebunch wheatgrass at a site located approximately 20 km from the site of this study. These authors reported that bluebunch wheatgrass responded in both percentage protein and yield to applications of 16.8, 33.6, and 67.2 kg/ha (15, 30, and 60 lbs/acre), respectively, of ammonium nitrate fertilizer. Although differences in ammonium nitrate encountered between sites in the present study are within this range, no difference in forage nitrogen occurred. Although significant, the differences in nitrogen content found by Mason and Miltimore (1959) equaled approximately only 10 percent of the absolute increase between 16.8 and 33.6 kg/ha. In a subsequent trial, Mason and Miltimore (1964) found that fertilizer applied at 28 kg/ha (25 lb/acre) increased foliar nitrogen content to only 0.79 percent, relative to 0.73 percent with no fertilization. Therefore, the current similarity in foliage nitrogen content of bluebunch wheatgrass on canopy and interspace soils is consistent with previous work in British Columbia.

Cheatgrass and Bluebunch Wheatgrass

Much of the interest in this study arose from reports of substantially higher foliar nitrogen concentrations of cheatgrass plants growing beneath shrub canopy microhabitats; hence, the question, "Why does cheatgrass show a response to unequal distribution of soil nitrogen while bluebunch wheatgrass does not?"

Cheatgrass, a vigorous, weedy, annual species, probably outcompetes bluebunch wheatgrass for soil nitrogen. Cheatgrass germinates with resumption of moist conditions in the fall, then overwinters as a seedling until spring. Cheatgrass initiates rapid growth early in the spring and sets seed by late June (Klemmedson and Smith 1964). Periods of active cheatgrass growth correspond with portions of the year when conditions are most suitable for mineralization. This fact, coupled with its extensive root system, provides cheatgrass with an efficient system for uptake of soil nitrogen. Alternatively, bluebunch wheatgrass initiates growth more slowly in the spring and does not respond as quickly to fall moisture. By the time this perennial grass begins seeking available nitrogen, much of the nitrogen will have been removed by earlier growing plants such as cheatgrass.

Additionally, cheatgrass may even be a nitrification inhibitor. Under laboratory conditions, root extracts of this plant inhibited the activity of Nitrosomonas and Nitrobacter by 9 and 25 percent, respectively (Neale 1969), suggesting that cheatgrass may be primarily a user of ammonium for nitrogen nutrition. Kline and McKell (1974) attributed increased growth of cheatgrass under sagebrush canopies to a better nitrogen

supply. If cheatgrass and sagebrush both inhibit nitrification of this increased supply of nitrogen, and if cheatgrass actually does utilize ammonium more readily than nitrates, then cheatgrass would indeed benefit from sagebrush canopy soils, which the current study shows to be relatively rich in ammonium. Therefore, the lack of response of foliar nitrogen in bluebunch wheatgrass on canopy soil sites may be due to (1) competition with sagebrush for moisture and nutrients, or (2) the inability of bluebunch wheatgrass to utilize large quantities of ammonium.

Summary and Conclusions

Sagebrush communities in British Columbia demonstrate patterning of soil total nitrogen, with higher concentrations found in under-canopy soils than in interspace zones. Ammonium nitrogen was also more prevalent at the canopy location, whereas nitrate nitrogen was significantly more concentrated in the interspace soils. Foliar nitrogen concentration of bluebunch wheatgrass did not differ between these two sites.

As the growing season progressed from May to August, foliar nitrogen content of bluebunch wheatgrass declined, as did soil ammonium nitrogen. In contrast, total soil nitrogen increased between these two sampling dates, while soil nitrate nitrogen concentration remained unchanged.

The discussion of these phenomena has been based upon a combination of biological knowledge and ecological speculation. The following hypotheses are suggested as future research topics which will help clarify and elucidate these speculations:

(1) Does sagebrush litter significantly inhibit the soil nitrification process?
(2) What form(s) of available nitrogen is (are) utilized by both weedy and beneficial plant species of the sagebrush community of interior British Columbia?
(3) Does the documented anisotrophic distribution of nitrogen benefit sagebrush relative to native perennial grasses?
(4) Can this competitive advantage of sagebrush be altered by judicious application of appropriate fertilizers?

Answers to these questions will provide a more complete understanding of the ecological relationships among sagebrush, soil fertility, and other botanical components of the arid rangelands of British Columbia. Such an understanding will also enhance our ability to manage these lands efficiently for a variety of resource products, as well as promote continued improvement in range condition.

Literature Cited

Blackburn, W. H., and C. M. Skau. 1974. Infiltration rates and sediment production of selected plant communities in Nevada. J. Range Manage. 27: 476-480.

Bremner, J. M. 1965. Total nitrogen, pp. 1149-1178 *in* C. A. Black (ed.). Methods of Soil Analysis, Part 2. Am. Soc. Agron., Madison, Wis.

Charley, J. L. 1977. Mineral cycling in rangeland ecosystems, pp. 216-256 *in* R. Sosebee (ed.). Rangeland Plant Physiology. Soc. for Range Manage., Denver, Colo.

———, and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems in Utah. J. Ecol. 63: 945-963.

———, and ———. 1977. Micropatterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems in Utah. Soil Biol. Biochem. 9: 357-365.

Daubenmire, R. 1975. Ecology of *Artemisia tridentata* subsp. *tridentata* in the State of Washington. Northw. Sci. 49: 24-35.

Environment Canada (Atmospheric Environment Service). 1974. Climate of British Columbia: Tables of Temperature and Precipitation. Climatic Normals 1941-1970. British Columbia Dept. of Agric.

Fulgham, P. T. Y., B. Klubek, and J. Skujins. 1975. Differential inhibition of nitrification in desert shrub communities. Annual Meeting of the Amer. Soc. for Microbiol. (Abstr.)

Garcia-Moya, E., and C. M. McKell. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecol. 51: 81-88.
Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest: An Illustrated Manual. Univ. of Wash. Press, Seattle.
Jackson, M. L. 1958. Soil Chemical Analysis. Prentice-Hall, New Jersey.
Kline, L. G., and C. M. McKell. 1974. Role of Annual Grasses and Shrubs in Nutrient Cycling of Great Basin Plant Communities. US/IBP Desert Biome Res. Memo. RM 74-14.
Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). Botanical Rev. 30: 226-262.
Mason, J. L., and J. E. Miltimore. 1959. Increase in yield and protein content of native bluebunch wheatgrass from nitrogen fertilization. Can. J. Plant Sci. 39: 501-504.
———, and ———. 1964. Effect of nitrogen content of beardless wheatgrass on yield response to nitrogen fertilization. J. Range Manage. 17: 145-147.
Neale, J. L. 1969. Inhibition of nitrifying bacteria by grass and forb root extracts. Can J. Microbiol. 15: 633-635.
Rickard, W. H., J. F. Cline, and R. O. Gilbert. 1973. Soil beneath halophytes and its influence upon the growth of cheatgrass. Northw. Sci. 47: 213-217.
———, and R. F. Keough. 1968. Soil-plant relationships of two steppe desert shrubs. Pl. Soil. 29: 205-212.
Rixon, A. J. 1971. Oxygen uptake and nitrification by soil within a grazed *Atriplex vesicaria* community in semiarid rangeland. J. Range Manage. 24: 435-439.
Tabler, R. D. 1964. The root system of *Artemisia tridentata* at 9,500 feet in Wyoming. Ecol. 45: 633-636.
Tiedmann, A. R., and J. O. Klemmedson. 1973a. Effect of mesquite on physical and chemical properties of the soil. J. Range Manage. 26: 27-29.
———, and ———. 1973b. Nutrient availability in desert grassland soils under mesquite (*Prosopis juliflora*) trees and adjacent open areas. Soil Sci. Amer. Proc. 37: 107-111.
Wallace, A., E. M. Romney, G. E. Kleinkopf, and S. M. Soufi. 1978. Uptake of mineral forms of nitrogen by desert plants, pp. 130-151 *in* N. E. West and J. Skujins (eds.). Nitrogen in Desert Ecosystems. Dowden, Hutchinson and Ross, Stroudsberg, Pa.

Received June 26, 1981
Accepted for publication November 13, 1981

Steven R. Peterson[1]

College of Forestry, Wildlife, and Range Sciences
University of Idaho
Moscow, Idaho 83843

A Preliminary Survey of Forest Bird Communities in Northern Idaho[2]

Abstract

Bird communities were examined in the hemlock (*Tsuga heterophylla*)/pachistima (*Pachistima myrsinites*) and grand fir (*Abies grandis*)/pachistima (*Pachistima myrsinites*) habitat types of northern Idaho in 1975 and 1976. Highest number of species and highest densities of breeding birds utilized the tall shrub communities or the shrub communities mixed with conifers. Bird diversity was relatively low in recent clearcuts or very early successional stages, then rose rapidly and reached an asymptote. Several examples are given to illustrate species replacement as vegetative communities changed.

Introduction

Vegetation structure has long been recognized as an important factor determining habitat use by avian communities (MacArthur *et al.* 1962, Zeedyck and Evans 1975, and others). Major plant communities have been well mapped, and the general distribution of birds is well known (Cowley 1971). However, evolution has resulted in each species being uniquely adapted to a specific type or range of habitats and environmental conditions. These habitat tolerances for forest species of birds have not been well researched.

A good information base on successional stages used by wildlife could help forest resource managers predict the consequences to wildlife when specific treatments are used to modify various successional stages (Sundstrom 1978). This association would allow forest managers to translate standard forest inventories into habitat use priorities for specific species or groups of species (Thomas 1979). Opportunities for habitat improvement or preservation should develop from this data base, and, as Pengelly (1972) pointed out, the benefits to wildlife will then be achieved by good planning rather than by accident.

The goal of the research reported in this paper is to increase our knowledge of forest/bird community relationships so that forest planners can make better decisions with minimum conflict. Specifically, habitat use patterns of breeding birds in the hemlock/pachistima and grand fir/pachistima habitat types (hts) of northern Idaho were assessed by:

(1) establishing species presence in various vegetational life forms in these habitat types;

(2) estimating species densities in these life forms;

---

[1]Present address: Game Research, Game Division, Department of Fish and Game, P.O. Box 3-2000, Juneau, Alaska 99801.

[2]A contribution of U.S. Forest Service, Intermountain Forest and Range Experiment Station, Intensive Timber Culture Project (#44-364) and the University of Idaho, College of Forestry, Wildlife, and Range Sciences. Contribution No. 212, Forestry, Wildlife, and Range Experiment Station, University of Idaho.

Figure 1. Study areas established in the hemlock/pachistima and grand fir/pachistima habitat types.

(3) comparing species diversity; and
(4) examining bird species replacement in life forms that represented general successional stages.

Study Area

Two study areas were established (Fig. 1). One site was located along the south fork of the Clearwater River approximately 40 km south of Grangeville, Idaho; the other was situated on the Coeur d'Alene River about 56 km north of Kellogg. Both areas were logged intensively by the U.S. Forest Service. Vegetative descriptions of the habitat types follow those described by Daubenmire (1968:25).

Methods

Plot Establishment

Within each study area ten plots, each representing different vegetative life forms within the types, were established. These life forms varied from recently burned (within one year) clearcuts through different age classes of shrubfields as well as several older

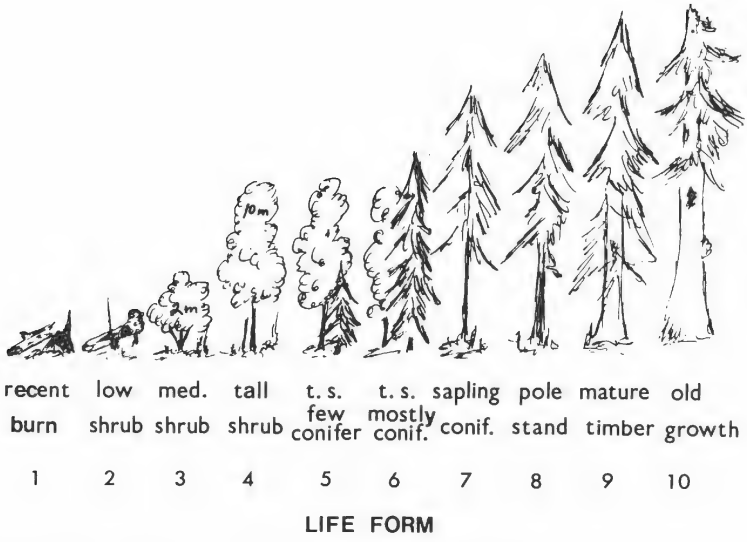


Figure 2. Vegetation life forms sampled for birds in hemlock/pachistima and grand fir/pachistima habitat types. The numbers are used as references in tabulated and graphed data.

age classes of conifer growth (Fig. 2). This figure should not be construed to represent true successional stages within the habitat types. Rather, they are life forms incorporating the youngest, oldest, and several arbitrary divisions of shrub/conifer habitat in between that more or less represent successional stages. Life forms were selected on a visual basis, and these were generally obvious. When these life forms are used in a graphical presentation of data later in the paper, they are referenced by the numbers 1-10 (youngest-oldest) to simplify reporting.

Several factors influenced the decision to establish a plot within a particular life form. First, the site had to be reasonably accessible; that is, 50 km or less from base camp, within several kilometers of at least one other plot, and within 100 m of vehicle access during the entire observation period. In regard to the latter, the first observation point was difficult to locate in dense shrubfields during pre-dawn hours unless the point was close to a well established trail or logging road. Second, the site needed to be as homogenous as possible; that is, I did not want more than one life form represented (such as stringers of timber in open areas, riparian vegetation in upland sites, open meadows in timbered areas, etc.). This criterion allowed sampling of birds specific to that life form and excluded birds characteristic of "edges." Third, the site had to be at least 16 ha (40 a) and if minimum in size, more or less square to fit the sampling design.

If the above criteria were met, the sampling design illustrated in Figure 3 was established. Based on preliminary observations, I concluded 25 m was the maximum limit that an observer could locate birds by sound and/or sight in dense or tall vegetation. Therefore, to keep the sampling design similar on all plots, this maximum observable distance in dense vegetation was used as the standard. Twenty-five observation

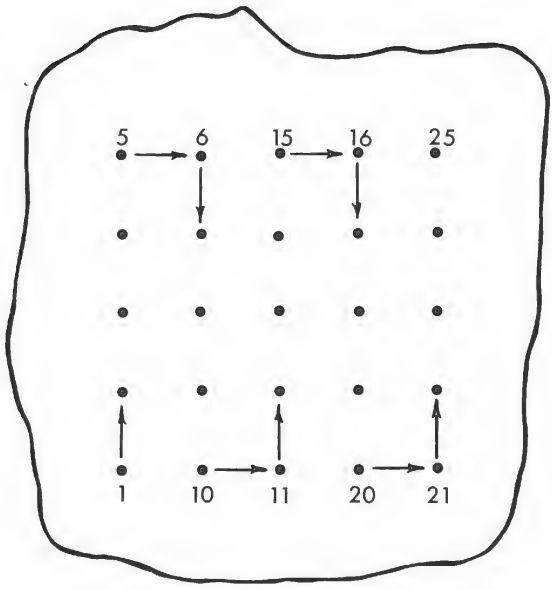


Figure 3. Sampling design for recording birds on selected sites in specific vegetative life forms.

points, each 50 m apart and $>$ 50 m from the edge of another life form, were marked with flagged surveyor's lath in a grid system. Selection of this number and system was a compromise based on the amount of time to be spent on the plot when the birds were singing, as well as the number, size, and physical shape of life forms available for sampling.

Field Procedures

If precipitation and wind were not sufficient to prevent hearing birds sing, an observer visited each plot once every two weeks. Observation commenced at point one, one-half hour before local sunrise, and proceeded in sequence until all 25 points were sampled. The observer recorded all birds seen or heard within 25 m of the sampling point during a 5 minute interval. Only one plot was sampled by a particular observer each day.

Results and Observations

Species Presence

Fifty-six species representing 19 families were recorded in the study plots during the summers of 1975 and 1976 (Table 1). The most prominent subfamilies of birds in the life forms sampled were sparrows (Emberizinae); finches and grosbeaks (Fringillidae); tyrant flycatchers (Fluvicolinae); wood warblers (Parulinae); and thrushes (Turdinae).

More species of birds occurred in the intermediate life forms (tall shrubfields or shrubfields with conifers starting to predominate in the overstory) than in either the

TABLE 1. Birds[1] per 100 ha found in different life forms sampled in the hemlock/pachistima and grand fir/pachistima habitat types of northern Idaho during the summers of 1975 and 1976.

Bird	Life Form 1	2	3	4	5	6	7	8	9	10
Charadrius vociferus	2									
Spizella breweri	7	10	4	1	4	3	9			
Sialia currucoides	19	47	13	1	7	7	3			
Empidonax oberholseri	4	3	7	3	11	23	7			
Selasphorus rufus	7	3	29	18	67	40	7			
Passerina amoena	3	5	12	14	10	22	13			
Colaptes auratus		7	4	5		4	13			
Bombycilla cedrorum				8						
Carduelis tristis					4					
Tyrannus verticalis					1					
Zenaida macroura					1					
Bonasa umbellus				1			5			
Falco sparverius				1		3				
Wilsonia pusilla			1	3	9					
Pipilo erythrophthalmus				3	14	2				
Pheucticus melanocephalus				4	15	5	4			
Cynocitta stelleri				1	3	2	9			
Archilochus alexandri			4	7	51	21	1			
Dendroica petechia			30	35	55	13	11			
Oporornis tolmiei	1		16	54	47	56	29		3	
Melospiza melodia			1	38			4			1
Corvus corax		1							1	
Myadestes townsendi		2			2		1	9		2
Accipiter gentilis		1					1			1
Buteo jamaicensis							1			
Turdus migratorius	36	38	18	49	91	55	58	10	27	14
Junco hyemalis	82	57	77	39	66	81	77	44	60	42
Dendroica coronata	5	3	9	16	37	19	27	18	19	4
Piranga ludoviciana	10	4	11	5	35	14	11	15	45	25
Spizella passerina	39	91	71	52	55	90	60	9	32	4
Carduelis pinus	3	45	19	1	11	4	7	26	33	63
Picoides villosus	2	3	5	1	8	9	3	7	13	10
Vireo solitarius	7		5	11	35	20	5		4	2
Empidonax traillii		1	9	18	25	3	12		1	3
Contopus borealis	1				10	1	5			3
Parus atricapillus		1	2		6	17	37	28	39	29
Catharus ustulatus			5	9	19	20	27	45	25	42
Empidonax hammondi	1		9	17	47	20	31	23	33	24
Passerella iliaca			2	15	22	1	5	3	3	1
Sphyrapicus varius				1	7	5	1		1	2
Troglodytes aedon				4			4	7		
Zonotrichia leucophrys							23			
Carpodacus cassinii					1	3		3		
Dendroica townsendi					11	5	8	3	3	
Parus gambeli	1				1	3	6	3	3	
Certhia americana						5	5	34	60	24
Regulus satrapa						19	5	27	11	27
Ixoreus naevius						23	11	26	7	30
Contopus sordidulus					1	3		8	1	12
Regulus calendula						3	3	8	4	13
Sitta canadensis						10	10	35	49	15
Parus rufescens						1		13	14	3
Dryocopus pileatus						3				4
Troglodytes troglodytes	3					3		10		
Perisoreus canadensis							2	3	1	
Dendroica virens								2		

[1]Scientific names follow 1957 ed. of AOU checklist and the thirty-second supplement to check-list found in Auk 1982, 99(3):1CC-16CC.

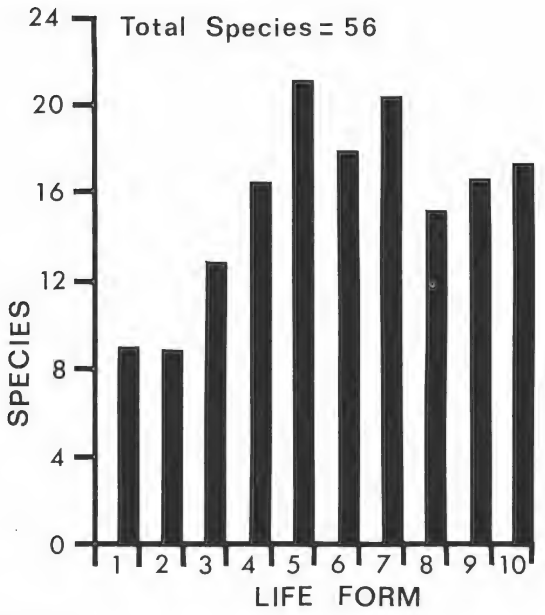


Figure 4. Numbers of bird species recorded in different vegetative life forms in hemlock/pachistima and grand fir/pachistima habitat types.

older age classes of conifers or recent clearcuts (Fig. 4). This figure represents a total average number of species from both parts of the study area and both years. An average of over 20 species was noted in the tall shrubfields, compared to 16 species in submature or oldgrowth stands and less than 10 in recent clearcuts or very short shrubfields. When these data are separated by locality (southern *vs* northern parts of the study area), or habitat type (grand fir/pachistima *vs* hemlock/pachistima), the trend is still supported.

Species Densities

Density estimates were computed from the birds observed within the 25 m radius of each observation point on the plots (4.9 ha sampled/plot). These densities were then converted to a 100 ha basis because this is a common denominator often used in bird survey work. The total average density was obtained by averaging the total birds recorded on each plot for the year; then similar plots (e.g., data from recent clearcuts in both parts of the study area) were combined. Next, these data were examined for basic trends. Presumably this density information represents minimal estimates, since the majority (ca 90 percent) of the observations were based on sound voiced by the territorial males.

The trend in total average birds/100 ha was similar to that observed for species in Figure 4. Not only did tall shrubfields and mixed conifer-shrubfields contain the most species, but these life forms also contained the most birds (Fig. 5). Also, older age classes of conifers had fewer birds present than the intermediate life forms, whereas new clearcuts and low shrubfields contained the fewest birds on the sites examined. Additional information on the density of specific species is presented in a later section on species replacement. Other data collected but not given in this paper suggest higher

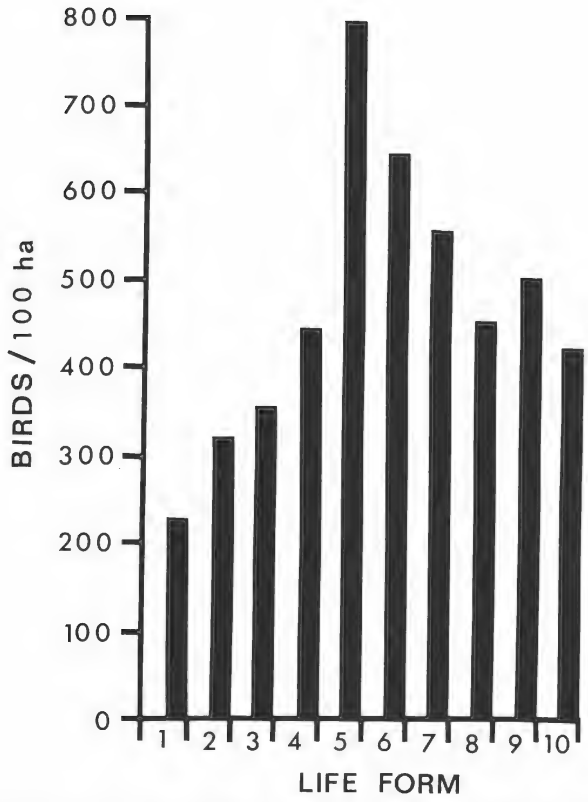


Figure 5. Bird densities recorded in different vegetative life forms in hemlock/pachistima and grand fir/pachistima habitat types.

bird densities, as well as more species, are present in the grand fir/pachistima than the hemlock/pachistima habitat types.

Species Diversity

Species diversity as measured by the Shannon-Weiner function ($H' = \Sigma p_i \log_e P_i$; where P_i is the population proportions of the various bird species) was relatively low in recent clearcuts and short shrubfields (Fig. 6). Bird diversity then rose rapidly and remained relatively constant throughout the rest of the life forms sampled.

Species Replacement

In general, certain species or groups of species were characteristic of specific life forms. Table 1 was arranged to exhibit the following trend: species characteristic of the younger life forms appear first; ubiquitous species that occurred throughout all life forms sampled appear in the middle; and species characteristic of the old classes of conifer stands occur last. Since the table shows birds/100 ha, the particular life form presumably best suited for a species that was recorded in several life forms should show the highest density. Data on species that were recorded in only one or two life forms, or where densities

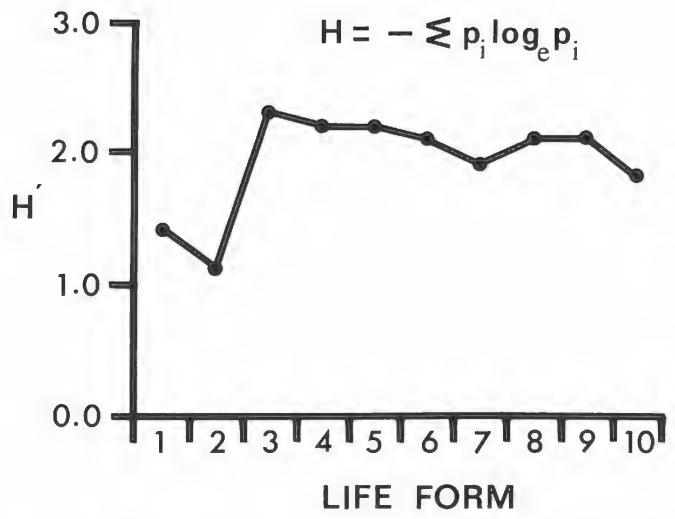


Figure 6. Bird species diversity calculated for different vegetative life forms in hemlock/pachistima and grand fir/pachistima habitat types.

were relatively low, should be viewed with caution. Sample sizes for these species are relatively low and may or may not reflect true densities.

Several species characteristic of the early, low growth life forms (recent clearcuts and low deciduous shrubs) were found. These included the Killdeer (*Charadrius vociferus*), Brewer's Sparrow (*Spizella breweri*), Mountain Bluebird (*Sialia currucoides*), Dusky Flycatcher (*Empidonax oberholseri*), Rufous Hummingbird (*Selasphorus rufus*), and Lazuli Bunting (*Passerina amoena*).

Relatively more species were characteristic of the older conifer stands than the younger life forms. The more common species included the Brown Creeper (*Certhia familiaris*), Golden-crowned Kinglet (*Regulus satrapa*), Mountain Chickadee (*Parus gambeli*), Varied Thrush (*Ixoreus naevius*), Western Wood Pewee (*Contopus sordidulus*), Townsend's Warbler (*Dendroica townsendi*), Ruby-crowned Kinglet (*Regulus calendula*), Red-breasted Nuthatch (*Sitta canadensis*), Chestnut-backed Chickadee (*Parus rufescens*), and Pileated Woodpecker (*Dryocopus pileatus*).

Species found in all forms studied included the American Robin (*Turdus migratorius*), Dark-eyed Junco (*Junco hyemalis*), Yellow-rumped Warbler (*Dendroica coronata*), Western Tanager (*Piranga ludoviciana*), Chipping Sparrow (*Spizella passerina*), Hairy Woodpecker (*Dendrocopos villosus*), and Pine Siskin (*Spinus pinus*).

Several species were restricted to shrubfields during the breeding season. In these life forms I observed American Kestrel (*Falco sparverius*), Ruffed Grouse (*Bonasa umbellus*), Wilson's Warbler (*Wilsonia pusilla*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Black-headed Grosbeak (*Pheucticus melanocephalus*), Black-chinned Hummingbird (*Archilochus alexandri*), and Yellow Warbler (*Dendroica petechia*).

Species replacement, as it relates to a specific family of birds, was examined and is illustrated with four species of thrushes (Fig. 7), tyrant flycatchers (Fig. 8), and wood warblers (Fig. 9).

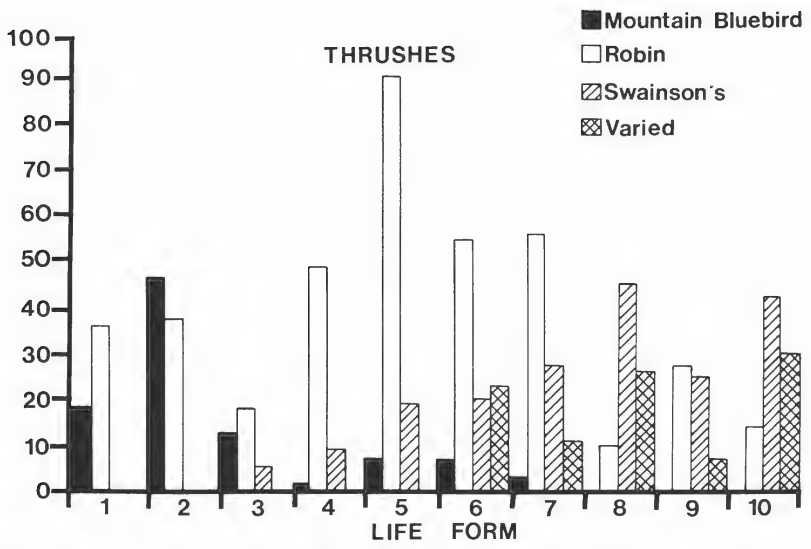


Figure 7. Densities of four members of the Turdidae recorded in different vegetative life forms in the hemlock/pachistima and grand fir/pachistima habitat types.

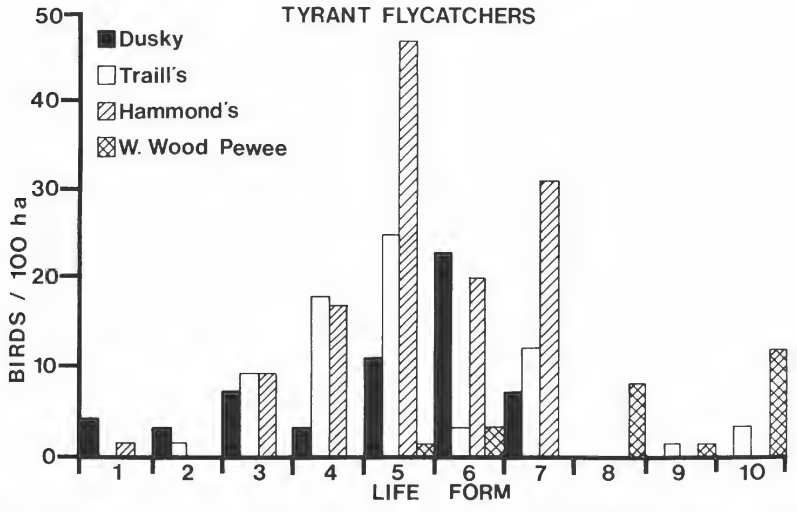


Figure 8. Densities of four members of the Tyrannidae recorded in different vegetative life forms in the hemlock/pachistima and grand fir/pachistima habitat types. Traill's Flycatcher is now known as the Willow Flycatcher (*Empidonax traillii*).

The thrush family exhibited a rather distinct species replacement pattern in the life forms studied. Soon after a burned clearcut became vegetated with young shrubs and forbs, Mountain Bluebirds reached their peak abundance on the site. When the shrubs reached several meters in height and conifers began to show in the understory,

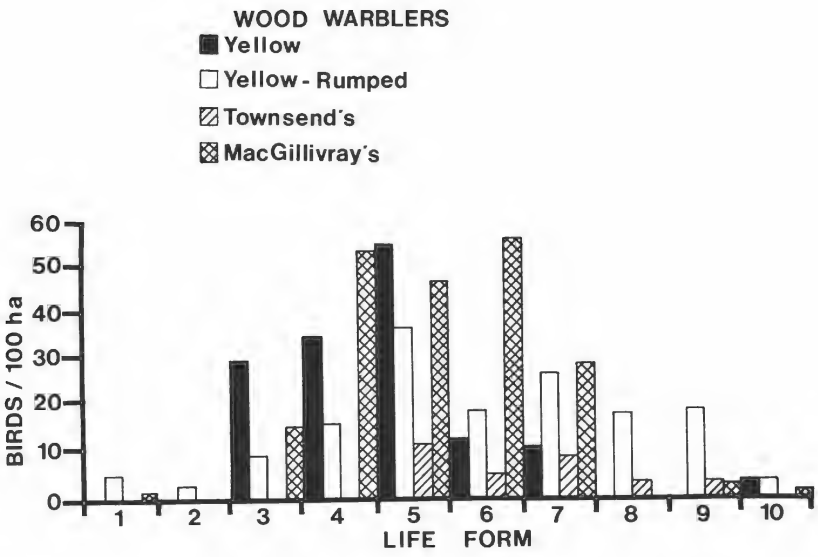


Figure 9. Densities of four members of the Parulidae recorded in different vegetative life forms in the hemlock/pachistima and grand fir/pachistima habitat types.

bluebird densities declined and the American Robin reached its peak abundance. I also noted Robins in recent clearcuts, but they were presumably using the open site for foraging. As the site became dominated by conifers, the Robin population was replaced first by Swainson's (*Hylocichla ustulata*) and later by the Varied Thrush. In any particular life form, the density of thrushes averaged about 75/100 ha, but the data suggest the density can vary from about 30 to well over 100 and consist of two to four species.

Species replacement in the tyrant flycatcher, as measured by gross vegetation structure in the grand fir/pachistima and hemlock/pachistima habitat types, was less obvious than in the thrushes. Dusky Flycatchers occurred on areas as long as deciduous vegetation was present. When this form of vegetation was absent and the stand well stocked with conifers, the Western Wood Pewee was present in relatively low numbers. Both the Willow (*Empidonax traillii*) and the Hammond's (*Empidonax hammondii*) flycatchers reached their peak densities each (25-50/100 ha) in the shrub/conifer life form but were found in most other life forms at relatively low densities.

The four species observed in the family of wood warblers showed the least tendency to be separated on gross vegetation structure. The highest densities occurred in the mixed shrub/conifer life forms. Few wood warblers were noted in the low or old growth life forms. Peak densities of wood warblers were higher than in the thrushes (ca 150 *vs* 75/100 ha), but average densities for all the life forms observed were lower (ca 50 *vs* 75/100 ha).

Discussion and Conclusions

Basically, the data support the concept that bird communities change as vegetative communities change. Several authors have examined this relationship, especially as

it relates to logging (Cowley 1971, Meslow and Wight 1975, Franzreb 1977, Austin and Perry 1979, and others). Presumably the presence or absence of a breeding species in a particular habitat is related to the ability of that species to exist in one or more types of habitat. Versatile species such as the American Robin, Dark-eyed Junco, or Chipping Sparrow can exist in a variety of northern Idaho upland habitats and are therefore the least sensitive to environmental change. On the other hand, several species recorded in this study including, for instance, Brewer's Sparrow and Brown Creeper, are unique to specific habitats and any major change to that habitat, whether it be caused by logging, fire, herbicide, or natural succession, will seriously affect populations of these species.

In many ways, the results of this study parallel the findings of other investigators working on bird communities in western conifer forests, but in other respects, the information conflicts with published data. I believe the underlying causes of these differences rest in the extensive development of the early to mid-successional shrub communities in northern Idaho. The importance of these stages to breeding birds is illustrated by not only the relatively large number of species present in these life forms but also by the overall density of birds in the shrub types.

Several studies have reported results on species composition, density, and diversity that are similar to those herein. Szaro and Balda (1979) also noted that openings made by logging resulted in an increase of those species which prefer more open habitat, as well as a decline or elimination of those species which require dense foliage. In addition, their results and those of this study contradict the theory that the greatest bird species diversity and population density are in over mature or climax forest. Similarly, Austin and Perry (1979) observed relatively few birds at low densities in mature lodgepole pine (*Pinus contorta*) stands of the Uinta Mountains, Utah. Conner and Adkisson (1975) found bluebirds to be most abundant on one-year-old clearcuts, but this species then decreased as the age of the clearcut increased. Presumably, this decrease is in response to the invading and/or growing vegetation.

The preceding authors also recorded a low breeding bird diversity shortly after clearcutting, but within a decade the diversity had increased considerably and became asymptotic. In the Douglas-fir (*Pseudotsuga menziesii*) forests of Oregon, as in the areas of northern Idaho, Dark-eyed Junco densities are about the same in freshly logged areas as in uncut forests.

In conclusion, I agree with Cowley's (1971) statement that any management practice (even doing nothing) or natural ecological process which affects the plant community will also affect the avian community. The silvicultural systems employed to manage northern Idaho forest communities can have a marked effect on bird populations. Elimination of the shrub stage by herbicide, cutting, or fire to promote conifer regeneration or seedling growth, will simplify the plant community and cause a severe reduction not only in the avian species that use the area but also in the number of birds occupying the site. Although bird habitat will not be destroyed per se in the process, these kinds of changes may not be in the best interest of the animal community as a whole.

Acknowledgments

I thank Robert Green, Dale Morman, Edward Rieckelman, and Gordon Bunch for their assistance in the bird survey.

Literature Cited

Austin, D. D., and M. L. Perry. 1979. Birds in six communities within a lodgepole pine forest. J. For. 77(9):584-586.

Conner, R. N., and C. S. Adkisson. 1975. Effects of clearcutting on the diversity of breeding birds. J. For. 73(12):781-785.

Cowley, R. D. 1971. Birds and forest management. Australian Forestry 35(4):234-250.

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. Pullman.

Franzreb, K. E. 1977. Bird population changes after timber harvesting of a mixed conifer forest in Arizona. USDA For. Serv. Res. Pap. RM-184.

MacArthur, R. H., J. W. McArthur, and J. Preer. 1962. On bird species diversity—prediction of bird census from habitat measurements. Amer. Natur. 96:167-174.

Meslow, E., and H. M. Wight. 1975. Avifauna and succession in Douglas-fir forests of the Pacific Northwest, pp. 266-271 *in* Proc. Symp. Management of Forest and Range Habitats for Nongame Birds. U.S. Dept. Agric. For. Serv. Gen. Tech. Rep. WO-1.

Pengelly, W. L. 1972. Clearcutting: detrimental aspects for wildlife resources. J. Soil and Water Conserv. 27:255-258.

Sundstrom, C. 1978. A Holistic Approach to Wildlife and Fish Habitat Management. Beaverhead National Forest.

Szaro, R. C., and R. P. Balda. 1979. Effects of Harvesting Ponderosa Pine on Nongame Bird Populations. Res. Pap. RM-212. Rocky Mtn. For. and Range Exp. Sta. USFS.

Thomas, J. W. (ed.). 1979. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handbk. No. 553. USDA.

Zeedyck, W. D., and K. E. Evans. 1975. Silvicultural options and habitat values in deciduous forests, pp. 115-127 *in* Proc. Symp. Management of Forest and Range Habitats for Nongame Birds. U.S. Dept. Agric. For. Serv. Gen. Tech. Rep. WO-1.

Received November 5, 1980

Accepted for publication January 9, 1981

William B. Collins

Agriculture Experiment Station
University of Alaska
Fairbanks, Alaska 99701

and

Philip J. Urness

College of Natural Resources
UMC 52
Utah State University
Logan, Utah 84322

Mule Deer and Elk Responses to Horsefly Attacks

Abstract

Mule deer (*Odocoileus hemionus hemionus*) and elk (*Cervus elaphus nelsoni*) are both greatly disturbed by horseflies. However, the two species exhibit distinctly different behaviors for coping with horsefly attacks. The compatibility of these behaviors with habitat preferences and other species-specific behaviors are discussed. Elk were found to attract relatively three times as many horseflies as did deer.

Little is known about the effect horseflies have on mule deer and elk behavior, although some researchers (Rue 1978, Murie 1951, Gruell and Roby 1976, Anderson 1958, Brazada 1953) believe that they substantially affect the summer distribution of these ungulates. We gained further insight into the disturbance effects of horseflies by observing tame, free-ranging deer and elk in the mountains of northern Utah. Observations were made during the course of a broader study which documented the daily activity patterns and habitat preferences of big game in aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) vegetation types (Collins 1979).

Daily activity patterns and the degree to which deer and elk were disturbed by flies were determined by scan sampling (Altmann 1974) tame, free-ranging individuals or groups of animals every 10 minutes for several 24-hour periods through the summers 1977 and 1978. Additionally, densities of horseflies at 1.5, 15, and 30 m from the animals were determined by counting the number of fly landings per 5 minutes on a 575 cm^2 hemisphere of a glossy black ball. A hand-held pole was used to suspend the ball 120 cm above the ground and 120 cm in front of the observer. The observer wore the same clothing during all observations to avoid differentially affecting the orientation of the insects (Bracken *et al.* 1962). All observations were made with the ball suspended in direct sunlight, the observer's back turned toward the sun.

Horseflies caused extreme disturbance to deer and elk during feeding and resting in the aspen type but were only occasionally disturbing in the lodgepole pine type, where flies were much less dense. The most abundant horsefly in the aspen type was *Hybomitra opaca*, a species which was present June through mid-August but most disturbing during July. *Tabanus punctifer* also occupied the type, but in too few numbers for reliable assessment of densities.

The activity of both species of flies was approximately the same in all subunits of the aspen type when ambient air temperature was 17° C or higher. Winds (measured up to 30 km/h at 120 cm height) and openness of habitat did not deter the flies; consequently, the deer and elk benefited little by moving from one subunit to another. The exception to this observation occurred when temperature lag in the forested subunit (attributable to shading) delayed the onset of fly activity and temporarily ($\leq$ 1.5 h) provided fly-free habitat after flies had become active in open subunits. At such times, the elk, which preferred feeding in meadow bottoms, readily moved to the forest. Deer typically were already feeding in the forested areas, and hence their distribution was less affected by flies. By contrast, the elk achieved considerable relief from mosquito attacks in the lodgepole pine type by moving from generally preferred resting sites to upland sites which were exposed to breezes (Collins *et al.* 1978). Darling (1937) found that red deer (*Cervus elaphus*) in Scotland moved to windy sites when they were harassed by small tabanids, but ran frantically when larger species became prevalent. *Hybomitra opaca* and *Tabanus punctifer* probably are able to persist under windy conditions because they have greater mass and flying strength than smaller flies and mosquitos.

During severe attacks the animals frequently ran to escape fly concentrations building up around them. In the case of deer, this behavior characteristically involved running from one bed to another, then quickly bedding down again. Generally, these movements were back and forth between 4-6 beds located within 40 to 50 m of each other. Such beds often became as much as 30 cm deep with repeated use. Deer preference for specific resting sites may represent predator-defense behavior, since greater familiarity with resting locale and possible escape routes is more essential for deer (which are typically solitary in summer) than for gregarious elk that benefit from group surveillance of surroundings.

Elk, on the other hand, did not remain in one general area when they ran from flies but moved several kilometers during the day. The distressed behavior of one elk usually stimulated the same behavior in others, and when one ran, all ran. Such social facilitation would never allow them to adopt the deer's fly-evading behavior of making short dashes between beds but may result in the elk finding areas which are more fly-free. Initially, we expected severe horsefly disturbance would lead to decreased grazing time. This was not the case, however, as the animals compensated for time lost during fly attacks by grazing more during the cooler part of the day and night.

Early in the study, elk were observed to rest more fitfully than deer during fly attacks. Measurements of fly densities at various distances from deer and elk confirmed our speculation that elk attracted relatively more flies than deer (Fig. 1). The only reason we can suggest for this observation is that the greater size of elk and their inclination to run relatively long distances during fly attacks lead to greater CO_2 production and higher body surface temperatures, both of which make the animals easier for the flies to locate (Anderson *et al.* 1974, Thorsteinson 1958). Thorsteinson (1958) suggested that motion may also act as an attractant to horseflies. Tashiro and Schwardt (1953) reported that, in cattle groups, the larger animals always attracted more flies than smaller ones. Others (Duncan and Vigne 1979, Freeland 1977) believe that animals in groups are less susceptible to horsefly attack than are individual animals.

Both deer and elk exhibited acute awareness of the different insect species pre-

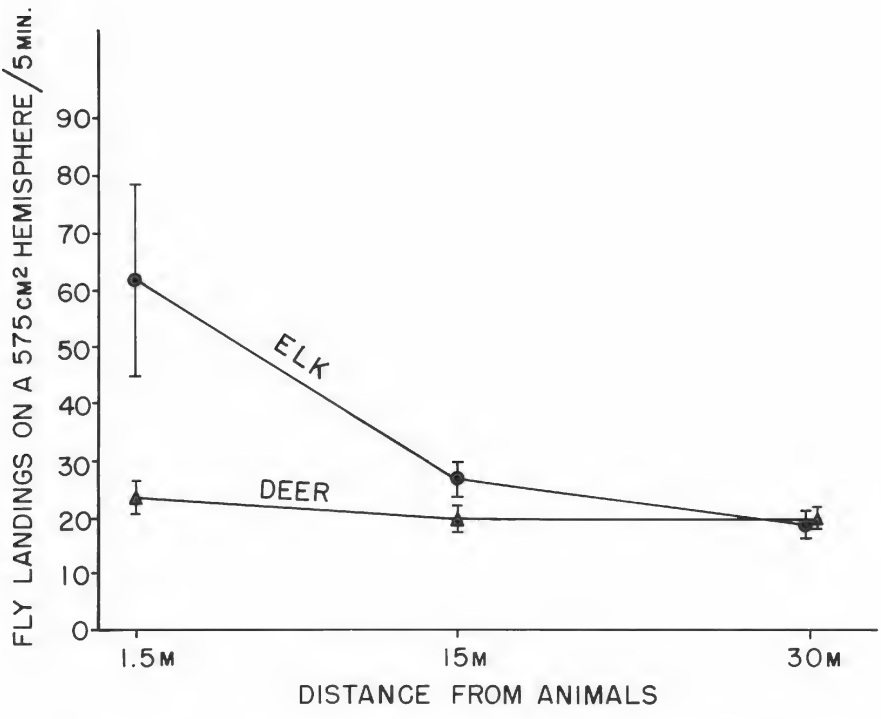


Figure 1. Fly activity at various distances from deer and elk; vertical bars represent standard deviations. The hemisphere was the visible side of a black ball suspended by a pole 120 cm from the observer and 120 cm above the ground.

sumably caused by differences in wing beat vibrations and resulting sounds. The presence of *Tabanus punctifer* within 2 or 3 m of the animals elicited wide-eyed alertness and often caused the animals to charge through vegetation where they normally would not travel. Individually or in low numbers, *Hybomitra opaca* were much less disturbing, although the deer and elk continually flicked their ears, stamped their legs or twitched that portion of their skin where *H. opaca* were hovering in search of a feeding site.

Neither deer nor elk made any movements to avoid white-faced hornets (*Vespula maculata*) that hovered near or landed on them. Close observation revealed that the wasps were methodically capturing horseflies (usually in mid-air), dismembering them and taking only the abdomens of their prey back to the hive. Wasps were efficient predators of horseflies, usually requiring only a few seconds to capture their prey. However, their benefit to deer and elk appeared marginal at high fly densities. Certainly the wasps benefited from the association, especially that with elk, since frequently as many as 150 flies were on or around them.

In conclusion, we believe that horseflies have a great direct impact on deer and elk behavior. This is not evident in terms of reduced grazing time but is manifest in a variety of comfort and escape movements which must be energetically costly to the

animals. In addition to that energy required for increased movement, increased muscle tonus and excitement associated with fly disturbance may also result in elevated metabolism; this should be investigated. Apparently elk are relatively more harassed by horseflies than are deer, and this factor may differentially favor deer rather than elk occupancy of some areas during the fly season.

Literature Cited

Altman, J. 1974. Observational study of behavior: Sampling methods. Behavior 49:227-265.

Anderson, C. C. 1958. The elk of Jackson Hole: A review of Jackson Hole elk studies. Wyo. Game and Fish Comm. Bull. No. 10.

Anderson, J. R., W. Olkowski, and J. B. Hoy. 1974. The response of tabanid species to CO_2-baited insect fly traps in northern California. Pan-Pacific Ent. 50:255-268.

Bracken, G. K., W. Hanec, and A. J. Thorsteinson. 1962. The orientation of horseflies and deer flies (Tabanidae:Diptera). II. The role of some visual factors in the attractiveness of decoy silhouettes. Can. J. Zool. 40:685-695.

Brazada, A. R. 1953. Elk migration patterns and some of the factors affecting movements in the Gallatin River Drainage, Montana. J. Wildl. Mgmt. 17(1):9-23.

Collins, W. B. 1979. Feeding behavior and habitat selection of deer and elk on northern Utah summer range. Utah State Univ., Logan, Ph.D. thesis.

———, P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. J. Wildl. Mgmt. 42(4):799-810.

Darling, F. F. 1937. A Herd of Red Deer. Oxford Univ. Press, London.

Duncan, P., and N. Vigne. 1979. The effect of group size in horses on the rates of attack by blood-sucking flies. Anim. Behav. 27:623-625.

Freeland, W. J. 1977. Blood sucking flies and primate polyspecific associations. Nature 269:801-802.

Gruell, G. E., and G. Roby. 1976. Elk habitat relationships before logging on Bridger-Teton National Forest, Wyoming, pp. 110-121 *in* M. S. Boyce and L. D. Hayden-Wing (eds.). Proceedings of the Elk-Logging-Roads Symposium. Univ. of Idaho; Forest, Wildlife and Range Exp. Sta.

Murie, O. 1951. The Elk of North America. The Stackpole Co., Harrisburg, Pa.

Rue, L. L., III. 1978. The Deer of North America. Crown Pub., Inc., New York.

Tashiro, H., and H. H. Schwardt. 1953. Biological studies of horseflies in New York. J. Econ. Ent. 46:813-822.

Thorsteinson, A. J. 1958. The orientation of horseflies and deer flies (Tabanidae:Diptera). I. The attractance of heat to tabanids. Ent. Exptl. et Appl. 1:191-196.

Received November 21, 1980
Accepted for publication December 24, 1980

Richard L. Knight[1]

Nongame Wildlife Program
Washington Department of Game
Olympia, Washington 95804

and

Dwight G. Smith

Department of Biology
Southern Connecticut State College
New Haven, Connecticut 06515

Summer Raptor Populations of a Washington Coulee

Abstract

Composition and spatial structure of a raptor community in a Washington coulee was studied for two years. Ten species totaling 41 and 38 pairs during 1978 and 1979, respectively, nested in the coulee. Red-tailed (*Buteo jamaicensis*) and Ferruginous (*Buteo regalis*) hawks were the most abundant diurnal raptors and Barn (*Tyto alba*) and Great Horned (*Bubo virginianus*) owls were the dominant nocturnal species. Analysis of intraspecific spatial relationships of nests showed that all species except the Barn Owl exhibited a uniform distribution. Interspecific distribution patterns were either uniform or random. The study area averaged 43.8 nests/100 km^2, suggesting good nesting habitat for Columbia Basin raptors.

Introduction

Sagebrush (*Artemisia* spp.) is estimated to have covered 58.7 to 109.3 million ha of land at one time in western America (Beetle 1960, Sturges 1973). Research on nongame wildlife species inhabiting the sagebrush community has been almost nonexistent, yet substantial parts of shrub-steppe have been, and are being, eliminated (Baker *et al.* 1976). To date, over 400,000 ha of Washington's Columbia Basin, much of which was shrub-steppe, has been irrigated with an additional 200,000 ha to be "reclaimed" to irrigated crops in the near future (USDI 1976a).

Within the Columbia Basin there exists approximately 3,900,000 ha of "channeled scablands" and "coulees." These basalt scablands consist of labyrinthine canyons, channels, basins, buttes, and coulees and were believed to have been carved by the Spokane Flood 18,000-20,000 years ago (USDI 1976b). Fitzner (1980) presented nesting densities of the raptor community for a large land area of varied topography and habitats in the Columbia Basin. Our impression was that whereas Fitzner's information accurately represented raptor nesting densities for heterogenous habitats and topography, channeled scablands and coulees provided small isolated islands of good nesting habitat, and would therefore be worth investigation. This paper presents population and productivity information of a raptor community in a coulee during 1978 and 1979.

Study Area and Methods

The study was conducted in a 6400 ha section of Esquatzel Coulee, Franklin County,

[1]Present address: Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706.

Figure 1. Location of Esquatzel Coulee study area, between Mesa and Connell, Washington.

Washington (Fig. 1). Esquatzel Coulee is 56 km long, with this study concentrating on a 13 km portion. Water on the study area consists of a pond, gravel pit, marsh, each less than 1 ha in size, and several streams formed from irrigation runoff which largely dry up during winter months.

A semiarid climate exists, with daytime summer temperatures averaging 32° C, and occasional subfreezing temperatures occurring during winter (USDI 1977). Annual mean precipitation at Eltopia (Fig. 1) is 21.1 cm. Prior to irrigation, vegetation in this area was classified as the *Artemisia tridentata-Agropyron spicatum* association (Daubenmire 1970). Overgrazing and farming have largely altered this plant community. At present, sagebrush and rabbitbrush (*Chrysothamnus* spp.) are the dominant shrubs, with cheatgrass (*Bromus tectorum*) the prevailing grass. In addition, mustards (*Brassica* spp.) and Russian thistle (*Salsola* sp.) are abundant.

This study was conducted from 1 October 1977 to 26 December 1979; intensive field work was performed from April to June each year. Population surveys were conducted monthly, and supplemental observations were collected at other sites. Raptor nests were found by systematically searching all potential nest sites, all of which were plotted on a map. Gaps between nests were then re-examined for possible missed nests or other signs of raptor activity.

At least two nest checks were made for each pair of raptors. The first visit was made in April to study territorial occupancy. Each observation was made as far from the

nests as possible to avoid hawk desertion during incubation and egg laying periods. Additional visits were made to obtain brood size and fledgling success.

Intraspecific and interspecific spatial patterns of raptor nests were analyzed using the Clark-Evans Nearest-Neighbor Model (1954), which compares the average minimum distance ($\bar{r}_A$) between nest sites with the expected distance ($\bar{r}_E$) assuming a uniform distribution of nests. The rates (R) of the two values are calculated as:

$$R = \frac{\bar{r}_A}{\bar{r}_E}$$

R values indicate distribution patterns with $R = 0$ for clumped, $R = 1$ for random, and $R = 2.15$ for uniform distribution patterns.

Results and Discussion

Including the Common Raven (*Corvus corax*) as an ecological counterpart of a raptor, there were 10 species of raptors nesting in Esquatzel Coulee (Table 1). A total of 41 and 38 pairs of raptors were located in the study area during 1978 and 1979, respectively. Diurnal raptors comprised the majority of the summer population, both in species and in overall numbers. In 1978, there were 26 pairs of seven species that were diurnal and 15 pairs of two species that were nocturnal. The situation changed little in 1979; one more nocturnal species, the Long-eared Owl (*Asio otus*), was added.

Two *Buteo* species, the Red-tailed Hawk (*Buteo jamaicensis*) and Ferruginous Hawk (*Buteo regalis*), and two nocturnal owls, the Great Horned Owl (*Bubo virginianus*) and Barn Owl (*Tyto alba*), were most abundant. Although there were marked changes in number of active nests for each species between years, there was no change in number of occupied territories, except for the Great Horned Owl (eight *vs.* six pairs). Thurow *et al.* (1980) have correctly pointed out that, whereas three species of the genus *Buteo* (Red-tailed Hawk, Ferruginous Hawk, and Swainson's Hawk (*Buteo swainsoni*)) are broadly sympatric throughout much of western North America, one species always seems to be uncommon. For example, the Red-tailed Hawk is the least common in the parkland zone of Alberta (Schmutz *et al.* 1980) and south-central Idaho (Thurow *et al.* 1980), whereas the Swainson's Hawk is least abundant in the eastern Great Basin of Idaho (Smith and Murphy 1973). Similarly, this study found that Red-tailed Hawks and Ferruginous Hawks were the common species. Although Swainson's Hawks were observed nesting outside Esquatzel Coulee, we have never observed one in the study area. Fitzner (1980), however, in an area 54 km southwest of this study, noted only one pair of Ferruginous Hawks nesting over a five-year period (pers. comm.), but Red-tailed Hawks and Swainson's Hawks were abundant. Fitzner (1980) and Schmutz *et al.* (1980) demonstrated that *Buteo* hawks showed degrees of ecological segregation by nesting sites and nesting habitats, even though they might opportunistically use the same resources when sympatric.

Ecological segregation of Red-tailed and Ferruginous hawks in Esquatzel Coulee was evident. Although both species used cliffs as nesting sites (Table 2), the average cliff height of 14.1 m for Red-tailed Hawks was significantly higher than the average of 7.8 m for Ferruginous Hawks ($t = 4.2$; $P < 0.05$). Red-tailed Hawks did show greater flexibility in nesting sites, land-use patterns of nesting sites, distances to roads and human habitation (Table 2), and food habits (pers. obsv.).

TABLE 1. Composition and productivity of Esquatzel Coulee raptor breeding populations, 1978 and 1979.[a]

Species	Territorial pairs		Number of territorial pairs of known breeding status		Total known active nests		Number of productive nests		Percentage of territorial pairs of known breeding status producing young		Number of young fledged		Number of young fledged per active nest		Number of young per territorial pair of known nesting status	
	1978	1979	1978	1979	1978	1979	1978	1979	1978	1979	1978	1979	1978	1979	1978	1979
Ferruginous Hawk	7	7	7	7	5	3	5	3	71.4	42.9	13	7	2.6	2.3	1.9	1.0
Red-tailed Hawk	8	8	7	8	6	5	5	4	71.4	50.0	13	6	2.2	1.2	1.9	0.8
Marsh Hawk	1	1	0	0	0	0	NK[b]	—	NK	NK	NK	NK	NK	NK	NK	NK
Prairie Falcon	1	1	1	1	1	0	1	0	100.0	0.0	3[c]	0	3.0	—	3.0	—
American Kestrel[d]	5	4	4	2	1	0	1	0	25.0	0.0	3	0	3.0	—	0.8	—
Great Horned Owl	8	6	6	6	3	3	3	3	50.0	50.0	9	8	3.0	2.7	1.5	1.3
Long-eared Owl	0	1	0	0	0	0	0	NK	0	NK	0	NK	—	NK	—	NK
Barn Owl[d]	7	7	2	1	2	1	2	NK	100.0	NK	6	NK	3.0	NK	3.0	NK
Burrowing Owl[d]	2	1	0	0	0	0	NK	NK	NK	NK	NK	NK	NK	NK	NK	NK
Common Raven	2	2	2	2	1	2	1	2	50.0	100.0	3	6	3.0	3.0	1.5	3.0
TOTAL	41	38	29	27	19	14	18	12	62.1	44.4	50	27	2.6	1.9	1.7	1.0

[a]Terminology defined in Postupalsky (1974).

[b]NK = not known.

[c]Nest contained 5 young; two were legally taken by falconers and 3 fledged.

[d]It was not always possible to determine if nests of all burrow and cavity nesting species were active.

TABLE 2. Summary of nest site and territory characteristics of raptors in Esquatzel Coulee, 1978 and 1979.

	Nest site				Territory					
	Structure				Land use		Average minimum distance (m)			
	Cliff	Tree	Other	Elevation (m)	Range	Farm	Permanent water	Primary road	Secondary road	Human habitation
Red-tailed Hawk	9	1	1[a]	275.7	8	3	741.2	2,196.2	516.8	1,550.6
Ferruginous Hawk	8	0	0	278.1	7	1	617.2	2,570.2	594.4	2,449.8
American Kestrel	5	0	0	253.0	4	1	1,091.2	1,859.3	390.1	2,535.9
Prairie Falcon	1	0	0	259.1	1	0	1,609.3	1,889.8	609.6	2,438.4
Barn Owl	11	0	0	278.5	10	1	989.2	1,486.6	382.4	2,554.8
Great Horned Owl	6	1	0	270.0	6	1	432.4	1,852.3	622.7	2,510.2
Burrowing Owl	0	0	2[b]	213.4	1	1	57.1	1,767.8	609.6	1,280.2
Common Raven	1	0	1[c]	243.8	2	0	914.5	2,249.4	244.0	2,438.4
TOTAL OR AVERAGE	41	2	4	258.9	39	8	806.5	1,983.9	496.2	2,219.8

[a]Transmission tower.
[b]Burrow.
[c]Railroad trestle.

Barn and Great Horned owls showed very little difference in nest site structure, land-use patterns of nesting sites, and distances to roads and human habitation (Table 2). Similarly, there was no difference between average nest structure height (12.3 m *vs* 12.6 m) or between average nest height (8.4 m *vs* 5.7 m) for Barn Owls and Great Horned Owls, respectively. Barn Owls have been present in eastern Washington only since the late 1950s (Stewart 1980), which possibly explains the lack of ecological segregation evidenced (see Knight and Jackman, in prep., for a more detailed discussion). In Fitzner's (1980) study, the two dominant nocturnal raptors were Great Horned Owls and Long-eared Owls, although Burrowing Owls (*Athene cunicularis*) were the most abundant in numbers.

Spatial relationships provide another method through which ecological segregation can be achieved, specifically interspecific territoriality (Orians and Willson 1964). We measured the distances between nests within and among species in order to test this factor (Table 3). For analysis, we selected raptor species with a minimum of nine nest distances within and among species. Intraspecific distributions of all raptor species, except the Barn Owl, show significant uniform distributions, indicating territorial establishment and maintenance of minimum nearest-neighbor distances (Table 3). This pattern is most strongly exhibited by Great Horned Owls ($R = 2.2$, $P < 0.01$) and Red-tailed Hawks ($R = 1.79$, $P < 0.01$). The random intraspecific distribution exhibited by Barn Owls may reflect reaction to Great Horned Owls, but this possibility is not supported by interspecific distances between the two most common owl species.

TABLE 3. Analysis of intraspecific and interspecific nesting raptor spatial distribution using the Clark-Evans' Nearest-Neighbor model.[a]

	Red-tailed Hawk	Ferruginous Hawk	American Kestrel	Barn Owl	Great Horned Owl
Red-tailed Hawk	1.79**				
Ferruginous Hawk	0.87	1.61**			
American Kestrel	0.90*	1.11	1.48**		
Barn Owl	0.89	1.46**	1.26*	1.05	
Great Horned Owl	0.95	1.13	1.58**	1.09	2.2**

[a]R values denote distribution patterns as follows: R = 1, random; R = 0, clumped; and R = 2.15, uniform.

*Significant at 0.05.

**Significant at 0.01.

Interspecific spatial patterns of nesting raptors were also examined (Table 3). Red-tailed Hawks showed random distribution patterns with Ferruginous Hawks, Barn Owls, and Great Horned Owls. Ferruginous Hawks, on the other hand, showed uniform distribution patterns with American Kestrels (*Falco sparverius*), Great Horned Owls, and Barn Owls, but only the latter was significant ($R = 1.46$, $P < 0.01$). The uniform distribution of American Kestrels with Barn Owls and Great Horned Owls may reflect predation of kestrels by the owls (Foster 1973). Avoidance of Barn Owls from predation by Great Horned Owls may also explain the uniform, but non-significant distribution observed between those two species (Knight and Jackman, in prep.).

Fitzner (1980) listed and discussed different nesting densities of raptor communities in the western United States. Raptor nesting density in the Birds of Prey Natural Area in southern Idaho was 181.0 nests/100 km^2. This density is considered to be optimum nesting habitat. The Hanford site, which is 54 km southwest of our study area, had a

density of 5.8 nests/100 km^2. Fitzner believes these differences more accurately reflect the density of a raptor community over a large land area of varied topography. Esquatzel Coulee during the two years of this study averaged 43.8 nests/100 km^2. Because of its relative isolation and abundant clifflines, Esquatzel Coulee provides near optimum nesting habitat.

Acknowledgments

We acknowledge the following persons who reviewed and commented on this paper: Clifford M. Anderson, Robert G. Anthony, Richard E. Fitzner, William J. Mader, John R. Patterson, Steve W. Platt, Carroll A. Rieck, Karen Steenhof, and John W. Weber.

We owe a special thanks to Herb Camp and his sons for allowing access to their land and for their patient hospitality during the study. Doug Weschler is kindly remembered for his initial idea of conducting research in Washington's coulees. Dana Ryan and Leonard Steiner are gratefully acknowledged for their interest and support throughout the two years of field work. Numerous individuals, too many to mention, provided field assistance and contributed greatly to this study. We thank Barbara Aukerman and Brigitte Nelson for typing the manuscript, Sue Peterson for preparing the figure, and Francis E. Jensen for the weather data. Lastly to Carroll A. Rieck, Supervisor of Washington's Nongame Wildlife Program, we pay special thanks for his guidance and encouragement throughout the study.

Literature Cited

Baker, M. F., R. L. Eng, J. S. Gashwiler, M. H. Schroeder, and C. E. Braun. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bull. 88:165-171.

Beetle, A. A. 1960. A Study of Sagebrush. The Section *Tridentatae* of *Artemisia*. Wyo. Agr. Expt. Sta. Bull. 368.

Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Wash. Agr. Expt. Sta. Tech. Bull. 62.

Fitzner, R. E. 1980. Impacts of a nuclear energy facility on raptorial birds, pp. 9-33 *in* R. P. Howard and J. F. Gore (eds.). Proceedings of a Workshop on Raptors and Energy Development. Boise.

Foster, J. H. 1973. Nesting Ecology and Selective Feeding of Great Horned Owls in the Palouse. Washington State Univ., Pullman. M.S. thesis.

Knight, R. L., and R. E. Jackman. In prep. Ecological segregation of Barn and Great Horned owls in a Washington coulee.

Orians, G., and M. F. Willson. 1964. Interspecific territories of birds. Ecology 45:736-745.

Postupalsky, S. 1974. Raptor reproductive success: Some problems with methods, criteria and terminology, pp. 21-31 *in* F. N. Hamerstrom, Jr., B. E. Harrell, and R. R. Olendorff (eds.). Management of Raptors, Raptor Res. Rept. No. 2.

Schmutz, J. K., S. M. Schmutz, and D. A. Boag. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. Can J. Zool. 58:1075-1089.

Smith, D. G., and J. R. Murphy. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. BYU Biol. Serv. 18(3):1-76.

Stewart, P. A. 1980. Population trends of Barn Owls in North America. American Birds 34:698-700.

Sturges, D. L. 1973. Soil moisture response to spraying big sagebrush the year of treatment. J. Range Manage. 26:444-447.

Thurow, T. L., C. M. White, R. P. Howard, and J. F. Sullivan. 1980. Raptor Ecology of Raft River Valley, Idaho. EG&G Idaho, Inc., Idaho Falls.

United States Department of the Interior. 1976a. Final Environmental Statement: Proposed Columbia Basin Project, Washington. U.S. Bur. Reclam., Washington, D.C.

———. 1976b. The Channeled Scablands of Eastern Washington: The Geologic Story of the Spokane Flood. USGS:INF-72-2(RI).

———. 1977. Esquatzel Coulee Wasteway: Draft Environmental Impact Statement. U.S. Bur. Reclam. Boise.

Received December 22, 1980
Accepted for publication March 16, 1981

Dale E. Toweill[1]

Oregon Department of Fish and Wildlife
P.O. Box 8
Hines, Oregon 97738

Winter Foods of Eastern Oregon Bobcats

Abstract

Food items of 102 bobcats (*Lynx rufus*) harvested by trappers and hunters in eastern Oregon during January 1980 were identified. Voles, rabbits and hares, and mice and woodrats were the most important items in the diet by frequency of occurrence and were found in 35, 34, and 29 percent of the sample, respectively. Birds (13 percent) and porcupines (6 percent) were of lesser importance. Female bobcats fed upon rabbits and hares to a greater extent than did males. Bobcats less than one year old took a higher percentage of mice and woodrats and birds, and a lower percentage of rabbits and hares, than older bobcats.

Introduction

Although bobcat food habits have been documented widely throughout the animal's range (Toweill 1979), only Bailey (1936) has presented food habits data for the species in eastern Oregon. He reported a high incidence of domestic sheep among food items of bobcats trapped, largely in response to animal damage complaints, during a peak in the sheep industry in eastern Oregon. More recently, deCalesta (1978) found no documented losses of sheep to bobcats in eastern Oregon while examining predation losses to livestock. Although Bailey did not report remains of domestic cattle in the bobcat diet, deCalesta reported that bobcats accounted for 5.5 percent of all predation losses of cattle in eastern Oregon. Bobcat predation was found to be a major cause of mule deer fawn mortality on Oregon's Steens Mountain (Tainer 1975, Ebert 1976), accounting for 18 percent of 99 documented fawn mortalities resulting from predation during the period 1971-1979 (Trainer *et al.* 1981).

After a two year moratorium on bobcat harvest in eastern Oregon in 1977-78 and 1978-79, limited harvest by hunters and trappers was allowed in January 1980. Persons successful in harvesting a bobcat were requested to present the skinned carcass to personnel of the Oregon Department of Fish and Wildlife. Such carcasses form the basis of this sample.

Objectives of this study were to document food habits of bobcats in eastern Oregon during a mid-winter period when food availability was at a minimum and to study differences in the diet of bobcats by sex and age. Data gathered were expected to reveal what prey species were important to survival of bobcats during winter.

Study Area

The collection area encompassed all of Oregon lying east of the summit of the Cascade Mountain Range. Diverse in habitat, the area included five of the physiographic provinces

[1]Present address: Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331.

described by Franklin and Dyrness (1973): the Columbia Basin, the Blue Mountains, the High Lava Plains, the Owyhee Upland, and the Basin and Range Provinces. Vegetation ranged from shrub-steppe to alpine.

Climate was essentially continental; January mean maximum temperatures ranged from −1 to 5°C (30 to 40°F) and January mean minimum temperatures ranged from −14 to −4°C (10 to 25°F). Winter (December through February) precipitation averaged from less than 5 cm to about 10 cm (Highsmith and Kimerling 1979).

Methods

Skinned bobcat carcasses were presented to personnel of the Oregon Department of Fish and Wildlife by hunters and trappers and were frozen until examination. Contents of stomachs and intestines were separated upon evisceration and analyzed separately. Analysis followed procedures suggested by Korschgen (1971), with the exception that intestinal contents were not weighed; stomach contents were weighed to 0.1 g. Following initial examination, all food items were preserved in 10 percent formalin; each sample was examined on at least two occasions to ensure that minute items were not missed.

Identification of food items was based primarily on comparisons with a reference collection and use of hair keys (Mayer 1952, Stains 1958, Adorjan and Kolenosky 1969).

Although stomach and intestinal contents were examined separately, results were combined for analysis. For example, if remains of a rabbit were found in both the stomach and intestine of one bobcat, they would be counted as one occurence of that food item. If a mouse was also found, but in the stomach only, it too was listed as one occurrence.

Results and Discussion

A total of 117 bobcat carcasses, 16 percent of the 753 bobcats reported harvested by fur takers in eastern Oregon in 1980, was examined. Food items were present in 102 (87 percent). Of 98 carcasses for which both the stomach and intestinal contents were examined (intestines had been removed from 4 animals prior to analysis), 47 percent had the same food items in both the stomach and intestines, whereas 28 percent had different food items in the stomach from those in the intestines. Food items were found in the stomach only in 11 percent and in the intestines only in 14 percent of the sample (Table 1).

Mean weight of stomach contents was 60.5g ($n = 117$), which included weight of gastrointestinal parasites and litter ingested while bobcats were held in traps.

Voles, rabbits and hares, and mice and woodrats were the most important items in the winter diet of eastern Oregon bobcats occurring in 35, 34, and 20 percent of the sample, respectively (Table 1). This prey composition was similar to that obtained in year-around food habits studies from Oregon (Bailey 1936, Nussbaum and Maser 1975) and other western states (Grinnell *et al.* 1937, Schwartz and Mitchell 1945, Leach and Frazier 1963, Young 1958, Gashwiler *et al.* 1960, Bailey 1974, Jones and Smith 1979). Data presented by Young (1958) and Jones and Smith (1979) show that percentages of lagomorphs in the diet increased during winter in the western

TABLE 1. Frequency and percent occurrence of food items recovered from digestive tracts of bobcats taken during January 1980 in eastern Oregon.

Food item	Frequency of occurrence		Percent occurrence
	Stomach	Intestine	
REPTILE: **Crotalus viridus**	1	1	1
BIRDS:	10	10	13
Anas strepera	2	1	2
Anas carolinensis	1	0	1
Alectoris chukar	2	2	3
Lophortyx californica	1	1	1
Passeriformes Unident.	4	6	6
SHREWS: **Sorex** sp.	1	2	2
RABBITS AND HARES:	25	31	34
Sylvilagus nuttalli	6	6	7
Sylvilagus sp.	6	5	6
Lepus americanus	2	3	3
Lepus californicus	6	9	10
Leporidae Unident.	5	8	9
SQUIRRELS:	4	2	4
Spermophilus lateralis	1	1	1
Tamiasciurus hudsonicus	2	1	2
Spermophilus sp.	1	0	1
POCKET GOPHER: **Thomomys talpoides**	1	0	1
KANGAROO RAT: **Dipodomys** sp.	0	1	1
BEAVER: **Castor canadensis**	1[a]	0	1[a]
WOODRATS AND MICE:	26	18	29
Neotoma cinerea	19	15	21
Peromyscus crinitus	2	0	2
Peromyscus maniculatus	3	1	3
Cricetidae Unident.	2	2	4
VOLES:	25	28	35
Microtus montanus	5	3	6
Microtus longicaudus	1	0	1
Microtus sp.	19	25	29
OLD WORLD RATS AND MICE:	2	1	2
Rattus norvegicus	1	1	1
Mus musculus	1	0	1
PORCUPINE: **Erethizon dorsatum**	4	5	6
MUSTELIDS:	2	0	2
Mustela vison	1	0	1
Taxidea taxus	1	0	1
COYOTE: **Canis latrans**	1	1	1
MULE DEER: **Odocoileus hemionus**	3	1	3
DOMESTIC COW: **Bos taurus**	1	1	1
MAMMAL Unident.	2	1	2
MASTICATED GRASS	3	5	6

[a]Taken as carrion; carcass had been skinned.

United States, and the percentages of rodents generally remained high. Rabbits and squirrels dominated the winter diet of bobcats in Arkansas (Fritts and Sealander 1978).

Birds occurred in 13 percent of the digestive tracts examined. Chukar Partridge (*Alectoris chukar*), California Quail (*Lophortyx californica*), and passerine bird remains almost certainly represent birds killed by bobcats. Grinnell *et al.* (1937) found remains of quail in 33 (13 percent) of 257 bobcat stomachs collected in California; however, Leach and Frazier (1953), investigating the importance of bobcat predation on birds in areas of upland game bird concentration in California, reported that such predation was insignificant. Although no remains of Sage Grouse (*Centrocercus uro-*

phasianus) were found during this study, Bailey (1936) reported that Sage Grouse were among the most common items taken by bobcats in eastern Oregon; remains of Sage Grouse were found in 10 percent of his sample.

Remains of two Gadwalls (*Anas strepera*) and one Green-winged Teal (*Anas carolinensis*) were probably eaten as carrion. In each case, only skin, feathers, and internal organs of ducks were found in bobcat digestive tracts, and these remains probably represented parts discarded by waterfowl hunters.

Porcupines (*Erethizon dorsatum*) had been eaten by six bobcats. Other workers, particularly in the northern and eastern United States, have reported that porcupines were a staple of the bobcat diet (Rollings 1945, Pollack 1951, Westfall 1956).

Incidence of mule deer (*Odocoileus hemionus*) in the winter diet of bobcats was low (3 percent), as has been reported in other studies of bobcat foods in areas where mule deer are found (Bailey 1936, Schwartz and Mitchell 1945, Leach and Frazier 1953, Young 1958, Bailey 1972, Nussbaum and Maser 1975, Jones and Smith 1979). By contrast, Gashwiler *et al.* (1960) reported that mule deer (much of it believed to be carrion) comprised about one-third of the bobcat diet in Utah and Nevada. Evidence from Trainer *et al.* (1981) suggested that to some extent the degree of bobcat predation on deer was a seasonal phenomenon. They reported that bobcat predation accounted for 18 percent of all predation losses of radio-equipped mule deer fawns, but most (61 percent) occurred during the summer; only 11 percent of documented bobcat predation occurred during winter.

Among the more unusual items in the winter diet of eastern Oregon bobcats was a Great Basin rattlesnake (*Crotalus viridus*), most likely taken from an exposed hibernaculum in a cave or rocky recess. The mink (*Mustela vison*), badger (*Taxidea taxus*), and coyote (*Canis latrans*) may have been taken as carrion by the bobcat.

A single incidence of a bobcat having fed on a domestic cow (*Bos taurus*) was recorded. As the remains consisted of hair only, there was no basis for telling whether the animal was taken as carrion.

Rabbits and hares were fed upon more frequently by female bobcats than by males (Table 2), despite the significantly lighter ($P < 0.01$) body weight of females. Remains of rabbits and hares were found in 46 percent of the female bobcats examined, but in only 25 percent of the males. Similarly, Fritts and Sealander (1978) reported that rabbits comprised 46 percent of the female diet and 35 percent of the male diet in Arkansas. Voles, mice, and woodrats also comprised major proportions of the bobcat diet and occurred with approximately equal frequency between sexes in this study (Table 2). Prey size did not appear related to body size of female and male bobcats, suggesting that bobcats do not partition prey between sexes. Fritts and Sealander (1978) reported

TABLE 2. Frequency and percentage occurrence of major food items taken by female and male bobcats during January 1980 in eastern Oregon.

	Female (N=46)		Male (N=56)	
Food item	Frequency	Percent	Frequency	Percent
VOLES	14	30	22	39
RABBITS AND HARES	21	46	14	25
MICE AND WOODRATS	15	33	15	27
BIRDS	6	13	7	13
PORCUPINE	4	9	2	4

that females utilized cricetid rodents to a greater extent than did males, and suggested that differences in the diet of females and males may have been attributable to females hunting their smaller home range areas more intensively than wider-ranging males. Such a difference was not found in this study of winter foods of bobcats, suggesting that this phenomenon, if present, may be limited to periods of prey abundance.

Food items of bobcats less than one year old were compared with foods taken by older bobcats (Table 3). Young bobcats fed more heavily on mice, woodrats, and birds than older bobcats, whereas older bobcats took a larger percentage of rabbits and hares than younger animals. Voles, mice, and woodrats may have been easier for young bobcats to capture because of behavioral differences or body size. Fritts and Sealander (1978) suggested that juvenile bobcats fed more frequently on rats and mice than on larger and more agile prey in Arkansas.

TABLE 3. Frequency and percentage of food items taken by bobcats less than one year of age and bobcats older than one year of age during January 1980 in eastern Oregon.

	Young bobcats (N=27)		Adult bobcats (N=75)	
Food item	Frequency	Percent	Frequency	Percent
VOLES	10	37	26	35
RABBITS AND HARES	7	26	28	37
MICE AND WOODRATS	9	33	21	28
BIRDS	5	19	8	11
PORCUPINE	1	4	5	7

Conclusions

Food habits of bobcats during January in eastern Oregon were examined to document food habits when food availability was presumed to be minimal and to study differences in food habits by sex and age. Voles, rabbits and hares, and mice and woodrats were most important in the winter diet of eastern Oregon bobcats. Little use of deer or domestic stock as food of bobcats was found. Data suggested absence of prey partitioning between female and male bobcats. Bobcats less than one year old fed more heavily on mice and woodrats and birds than bobcats one year or older, suggesting the importance of small prey to kitten survival through the first year.

Acknowledgments

Sincere appreciation is extended to those hunters and trappers throughout Oregon who provided bobcat carcasses, and to the personnel of the Oregon Department of Fish and Wildlife who assisted in carcass collections. I also thank R. Denney, under whose direction the carcass-collection program originated, and C. E. Trainer, who encouraged the analysis. R. G. Anthony, D. S. deCalesta, and C. E. Trainer reviewed this manuscript and offered valuable suggestions.

Literature Cited

Adorjan, A. S., and G. B. Kolenosky. 1969. A Manual for the Identification of Hairs of Selected Ontario Mammals. Ontario Dep. Lands Forests, Res. Rep. (Wildl.) 90.

Bailey, T. N. 1972. Ecology of Bobcats with Special Reference to Social Organization, Univ. Idaho, Moscow, Ph.D. thesis.

———. 1974. Social organization in a bobcat population. J. Wildl. Manage. 38(3):435-446.

Bailey, V. 1936. The Mammals and Life Zones of Oregon. N. A. Fauna 55.

deCalesta, D. S. 1978. Documentation of Livestock Losses to Predators in Oregon. Spec. Rep. 501, Oregon State Univ. Ext. Serv., Corvallis.

Ebert, P. N. 1976. Recent changes in Oregon's mule deer population and management. Proc. West. Assoc. State Game Fish Comm. 56:408-413.
Franklin, J. F., and C T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
Fritts, S. H., and J. A. Sealander. 1978. Diets of bobcats in Arkansas with special reference to age and sex differences. J. Wildl. Manage. 42(3):533-539.
Gashwiler, J. S., W. L. Robinette, and O. W. Morris. 1960. Foods of bobcats in Utah and eastern Nevada. J. Wildl. Manage. 24(2):226-229.
Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-bearing Mammals of California. Univ. California Press, Berkeley.
Highsmith, R. M., Jr., and A. J. Kimerling. 1979. Atlas of the Pacific Northwest. Sixth ed. Oregon State Univ. Press, Corvallis.
Jones, J. H., and N. S. Smith. 1979. Bobcat density and prey selection in central Arizona. J. Wildl. Manage. 43(3):666-672.
Korschgen, L. J. 1971. Procedures for food-habits analyses, pp. 233-250 *in* Giles, R. H., Jr. Wildlife Management Techniques, third ed. The Wildlife Society, Washington, D.C.
Leach, H. R., and W. H. Frazier. 1953. A study on the possible extent of predation on heavy concentrations of Valley Quail with special reference to the bobcat. California Fish Game 39(4): 527-538.
Mayer, W. V. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. Am. Midl. Nat. 48(2):480-512.
Nussbaum, R. A., and C. Maser. 1975. Food habits of the bobcat, *Lynx rufus*, in the Coast and Cascade Ranges of western Oregon in relation to present management policies. Northw. Sci. 49(4):261-266.
Pollack, E. M. 1951. Food habits of the bobcat in the New England states. J. Wildl. Manage. 15(2): 209-213.
Rollings, C. T. 1945. Habits, foods, and parasites of the bobcat in Minnesota. J. Wildl. Manage. 9(2):131-145.
Schwartz, J. E., and G. E. Mitchell. 1945. The Roosevelt elk on the Olympic Penninsula, Washington. J. Wildl. Manage. 9(4):295-319.
Stains, H. J. 1958. Field key to guard hair of middle western furbearers. J. Wildl. Manage. 22(1): 95-97.
Toweill, D. E. 1979. Bobcat Populations, a Review of Available Literature. Oregon Dep. Fish Wildl. Info Rep. Ser., Wildlife. 79-2.
Trainer, C. E. 1975. Direct causes of mortality in mule deer fawns during summer and winter periods on Steens Mountain, Oregon—a progress report. Proc. West. Assoc. State Game Fish Comm. 55:163-170.
———, J. C. Lemos, T. P. Kistner, W. C. Lightfoot, and D. E. Toweill. 1981. Mortality of mule deer fawns in southeastern Oregon, 1968-1979. Wildl. Res. Rep. 10, Oregon Dep. Fish Wildl.
Westfall, C. Z. 1956. Foods eaten by bobcats in Maine. J. Wildl. Manage. 29(2):199-200.
Young, S. P. 1958. The Bobcat of North America. A. Stackpole Co., Harrisburg, PA, and the Wildlife Management Institute, Washington, D.C.

Received January 8, 1981
Accepted for publication March 11, 1981

Louise E. Jackson

Department of Botany
University of Washington
Seattle, Washington 98195

Comparison of Phenological Patterns in Prairie and Subalpine Meadow Communities

Abstract

In a lowland prairie community in western Washington, seven different phenological patterns occur, specialist pollinators are common, and plants vary in the length of their growing seasons. In a subalpine meadow community on nearby Mt. Rainier, only three different phenological patterns occur, most pollinators are generalists, and there is little difference between species in growing season length. Three differences in plant growth patterns appear to result from increasing growing season length: (1) temporal variability in environmental conditions during a long growing season leads to a greater diversity in plant life forms; (2) phenological stages are more separated in time, and their duration varies more among species in a community with a longer growing season; and (3) the staggering of flowering promotes insect pollinator specialization in the lowland prairie.

Introduction

Studies of plant phenology, the description of the timing and duration of stages in plant growth and development, have addressed a wide variety of topics. Those of ecological interest include the coevolution of flowering times with insect pollination (Mosquin 1971, Reader 1975, Heinrich 1976), the importance of the timing of growth in physiological autecology (Johnson and Caldwell 1974, Mooney and Chu 1974), and patterns of annual variation in flowering times within communities (Pitt and Heady 1978). In this study, the relationship between community-wide phenological patterns and the length of the growing season is examined by comparing phenological patterns of a lowland prairie community and a subalpine meadow community.

In high-elevation communities, the necessity of competing life cycles within a short period limits the diversity of growing strategies (Bliss 1956, Holway and Ward 1965), but in communities that can grow through most of the year, plant species with different phenological patterns can coexist (Pemadasa and Lovell 1974, Monasterio and Sarmiento 1976, Al-Mufti *et al.* 1977). In communities with long growing seasons, resource quality and availability frequently change as the season progresses, exposing resident plant species to a wide variety of environmental conditions. I hypothesized that environments with longer growing seasons should show: (1) more variability between community members in the timing and duration of vegetative growth; (2) greater separation between species in flowering times; and (3) a greater diversity of life forms. These hypotheses were tested by comparing life-form diversity, phenological characteristics, and pollination biology of herbaceous plants in two western Washington meadow communities: a lowland prairie where year-round growth is possible and a dry subalpine meadow with a snow-free period of about four months.

Methods

Study Areas

Both study areas are level meadows greater than 2.5 km^2 in area in which plants are of

similar stature. Sites were chosen for their topographic, soil, and microenvironmental homogeneity and the evenness of species distribution within communities, based on visual appraisal.

Scatter Creek Prairie (Scatter Creek Wildlife Recreation Area) is located in the Puget Sound lowlands (55 m elevation) 30 km south of Olympia, Washington (46°49′N 123°1′W) (Fig. 1). Rains continue with few interruptions through the winter and spring, but summers are warm and generally dry. Eurasian grasses dominate the prairie vegetation, but approximately equal numbers of Eurasian and native forb species are present. Though alien species are prevalent, natives are as well represented and the site is as little disturbed as any in the region.

Grand Park is a high plateau near Sunrise, Mt. Rainier National Park, at 1710 m elevation (46°58′N 121°41′W) (Fig. 1) approximately 100 km east of Scatter Creek Prairie. Freezing temperatures and snow cover predominate from October through May. Summer precipitation is typically low and the pumice soils are well drained. The meadow is characterized by dry meadow species of the Low Herbaceous Subalpine vegetation type (Henderson 1974). Composites make up 43 percent of the total vascular plant cover. No introduced species occur at Grand Park.

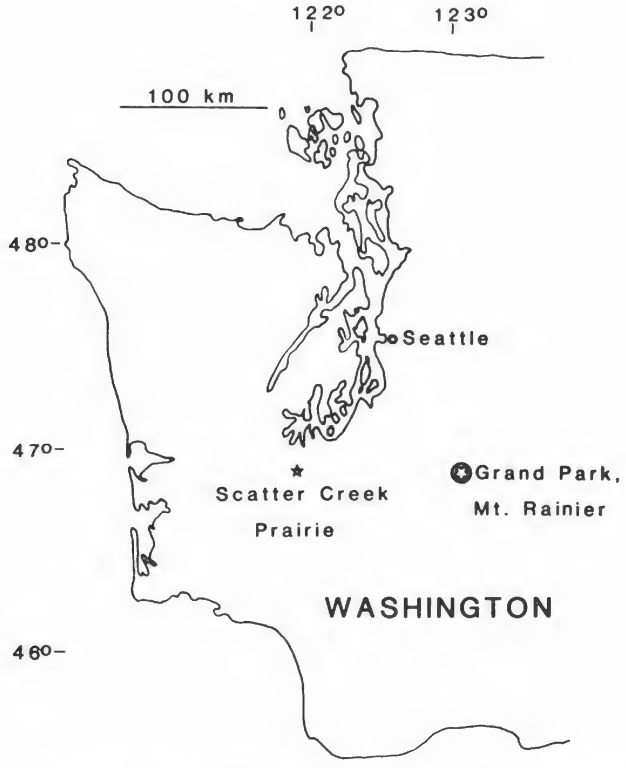


Figure 1. Map of Washington showing the Scatter Creek Prairie study site at 55 m elevation and the Grand Park, Mt. Rainier study site at 1710 m elevation.

Sampling

At the time of maximum cover at each site, average percent cover was estimated for each vascular plant species present in 25 1 m^2 plots spaced at 5 m intervals along two 60 m transects within each study area. Nomenclature is that of Hitchcock and Cronquist (1973), and plants were compared with specimens in the University of Washington Herbarium.

In 1977, in the center of each meadow, 25 0.1 m^2 plots were chosen for phenological evaluation within an area approximately 80 m in diameter. A different set of 25 plots was chosen semi-randomly on each visit by walking a random number of steps from the previous plot. Each individual plant in these plots was assigned to one of four developmental stages: vegetative growth (before the emergence of floral buds); floral bud emergence (only floral buds and no flowers present); flowering; and seed and fruit production. For the 14 most abundant species at the lowland prairie (seven entomophilous and seven grass species) and the 13 most abundant species at the subalpine meadow (nine entomophilous species and four graminoid species), means and standard deviations for the duration of these four periods were calculated. All herbaceous species in both communities with more than 0.4 percent cover were included.

Scatter Creek Prairie was visited at approximately 10-day intervals between February and August and at monthly intervals during the autumn and winter. The autumn and winter visits consisted only of qualitative assessments of phenology. At Grand Park, visits were made about once a week between late June (just after snowmelt) and late September (soon after the first winter snowfall).

Insect pollinator diversity, abundance, and constancy were observed during flowering periods in both communities. On each visit, pollinators were counted and individuals were followed. Relative abundance of each insect species during an approximate six-hour period was assessed using a rating system (+ = 1 individual, 1 = 2-4, 2 = 5-10, 3 = greater than 10). Voucher specimens were identified according to Borror *et al.* (1976) and Pyle (1974) and are in the author's collection. The percentage of enlarged ovules in approximately 25 seedforming flowers estimated seed set in the dominant species. The average number of developing ovules per fruit (or flower) multiplied by the average number of fruit producing flowers per plant gave the number of seeds per plant.

During 1978, quantitative phenological measurements were taken only during the flowering period, but qualitative observations were made throughout the entire growing seasons.

I used Reciprocal Averaging, an ordination method that simultaneously ordinates species and attributes by designating a rough gradient, and then cross-calibrating scores until they stabilize (Hill 1973) to determine the degree of similarity in peaks of phenological periods in the most dominant entomophilous herbaceous species of both communities. Attributes were the dates of peak of floral bud emergence, peak of flowering, and peak of seed and fruit production.

Results

Species Composition and Life Form Diversity

Cover values (percent) and pollen vectors (W = wind; S = specialist insects; G = generalist insects) are noted in Table 1 for the sampled species. Native or alien origin is given for prairie species.

TABLE 1. Cover of vascular plant species at the two study sites. Pollen vectors are abbreviated as W = wind, GP = generalist pollinating insects, SP = specialist pollinating insects. All plant species in the subalpine meadow are natives.

Scatter Creek Prairie Species	% cover	Pollen vector	Origin	Grand Park Subalpine Species	% cover	Pollen vector
Agrostis tenuis	37.7	W	Alien	**Aster alpigenus**	21.0	GP&SP
Camassia quamash	4.4	SP	Native	**Polygonum bistortoides**	10.2	GP
Vicia sativa	3.3	GP	Alien	**Festuca viridula**	9.2	W
Cytisus scoparius	2.9	GP	Alien	**Antennaria lanata**	6.1	GP
Agrostis diegoensis	2.7	W	Native	**Carex spectabilis**	5.4	W
Dactylis glomerata	2.1	W	Alien	**Danthonia intermedia**	2.8	W
Ranunculus occidentalis	1.8*	SP	Native	**Potentilla flabellifolia**	2.5	GP
Plantago lanceolata	1.6	**	Alien	**Potentilla diversifolia**	1.5	GP
Pteridium aquilinum	1.6	—	Native	**Gentiana calycosa**	1.4	GP
Hypochaeris radicata	1.5	GP	Alien	**Lupinus latifolius**	0.8	GP
Poa pratensis	1.3	W	Alien	**Vaccinium deliciosum**	0.8	@@
Anthoxanthum odoratum	1.0	W	Alien	**Trisetum spicatum**	0.5	W
Holcus lanatus	0.6	W	Alien	**Pedicularis contorta**	0.4	GP
Rubus ursinus	0.5	@@	Native	**Tauschia stricklandii**	0.3	GP
Potentilla gracilis	0.4	GP&SP	Native	**Aster ledophyllus**	0.3	GP
Arrhenatherum elatius	0.4	W	Alien	**Castilleja parviflora**	0.1	**
Eriophyllum lanatum	0.3	**	Native	**Erythronium grandiflorum**	+	**
Vicia hirsuta	0.2	**	Alien			
Rumex acetosella	0.2	**	Alien	**Penstemon procerus**	+	**
Aira praecox	0.2	W	Alien	**Phleum alpinum**	+	W
Hypericum perforatum	0.1	**	Alien	**Polygonum newberryi**	+	**
Danthonia californica	0.1	W	Native			
Achillea millefolium	+	**	Native			
Delphinium nuttallii	+	**	Native			
Festuca occidentalis	+	**	Native			
Senecio jacobaea	+	GP	Alien			
Solidago canadensis	+	**	Native			
Sysrinchium douglasii	+	**	Native			

*Cover determined earlier in the season.

**No pollinators observed.

@@No flowering occurred.

According to the Raunkiaer system of life-form classification (Raunkiaer 1934), 4 percent of the 28 species sampled at Scatter Creek Prairie are phanerophytes, 57 percent are hemicryptophytes, 32 percent are cryptophytes, and 7.2 percent are therophytes. There is less life form diversity in the 20 species at the subalpine site: 15 percent are chamaephytes, 70 percent are hemicryptophytes, and 15 percent are cryptophytes.

Phenology

Vegetative growth

At the lowland prairie, the majority of species exhibited a long period of vegetative growth early in the season before floral buds emerge (Fig. 2). Post-reproductive vegetative growth was minimal because almost all species become dormant during or shortly after seed dispersal. The fourteen most dominant, insect-pollinated species spent 8 $\pm$ 3 weeks in vegetative growth after quantitative measurements began in February. Both mean and variance are actually higher because some species are capable of winter growth (e.g., *Hypochaeris radicata* and *Plantago lanceolata*). Other vegetative growth strategies were illustrated by *Vicia sativa* and *Ranunculus occidentalis*, which underwent mid-summer dormancy but emerged in the fall; *Camassia quamash*, which flowered three weeks after leaves emerged; and *Potentilla gracilis, Solidago canadensis, Eriophyl-*

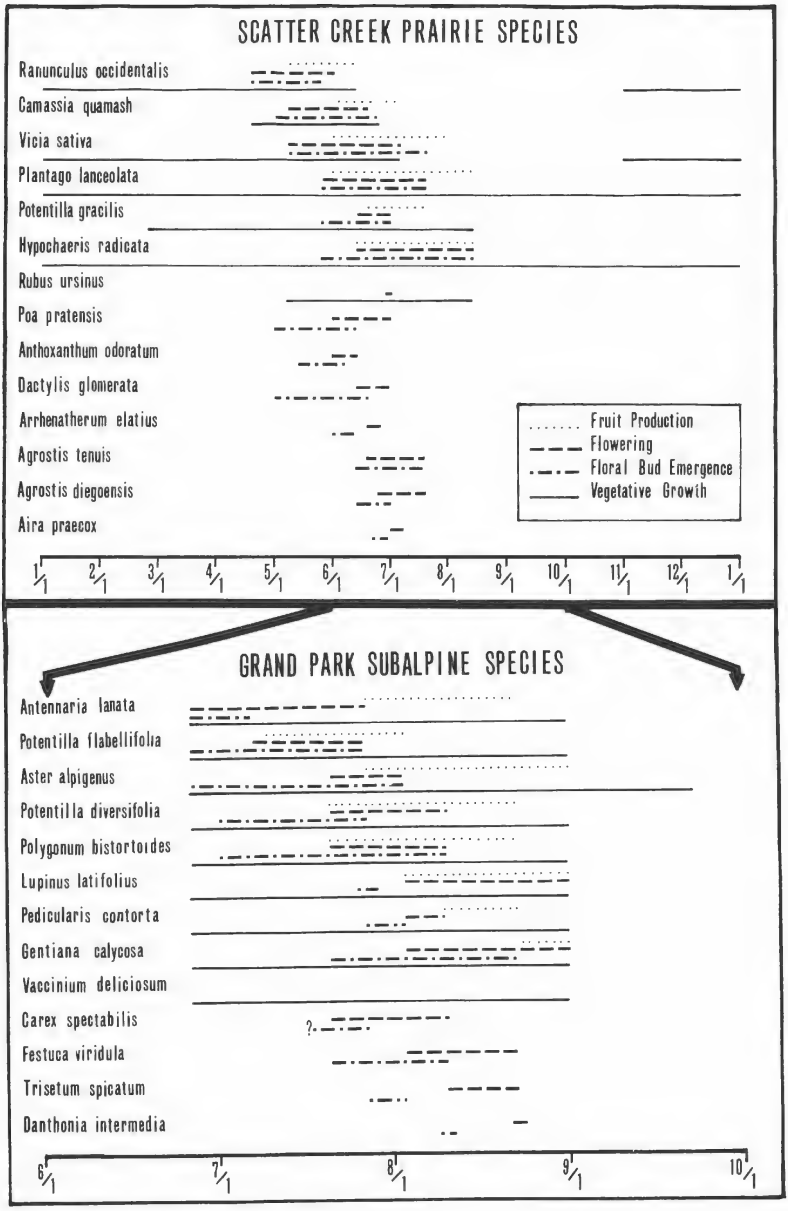


Figure 2. Phenological periods of species with greater than 0.3 percent cover at Scatter Creek Prairie and Grand Park, Mt. Rainier as determined from sampled plots. The dominant 13 species at each site are included. Species in insect and wind-pollinated groups are listed by their flowering times. Vegetative growth periods and fruit production periods are omitted for wind-pollinated species due to insufficient data. Note the change in time scale for the two sites.

lum lanatum, and *Rubus ursinus*, which emerged in mid-spring. Although not included in the field data, so not shown in Figure 2, the ten grass species also had long periods of pre-reproductive vegetative growth, sprouting as early as late autumn, and growing continuously through the winter.

At Grand Park, Mt. Rainier, little time was allotted to purely vegetative growth in those plants that flowered in 1977. Figure 2 shows that leaves and floral buds emerged almost simultaneously at the beginning of the season in the dominant insect-pollinated species with greater than 1.5 percent cover. Species that had delayed floral bud emergence but produced leaves soon after snow release were infrequent and made up less than 1.5 percent cover. However, graminoids remained vegetative until late July, one month longer than the dominant insect-pollinated species.

Floral bud emergence

At least 85 percent of the individuals of the prairie species produced floral buds. Exceptions were the geophyte *Camassia quamash* (65 percent) and the trailing vine *Rubus ursinus* (less than 10 percent). Floral bud production lasted from April to August (Fig. 2). Initiation of this phenological stage by dominant insect-pollinated species lasted longer than among dominant grasses, and the mean length of the bud-producing period was two weeks longer (6 ± 3 weeks) than in the grasses (4 ± 2 weeks).

At the subalpine site, 15 percent of all *Aster alpigenus, Polygonum bistortoides, Potentilla flabellifolia,* and *Antennaria lanata* individuals and 40 percent of all *Potentilla diversifolia* and *Gentiana calycosa* individuals produced floral buds. Overall, flowering appears to be a much less regular event for individuals in the subalpine meadow than in the prairie. The timing of floral bud emergence differed more in these plants than in the grasses, in which budding inflorescences were present for one month only between late July and late August. The mean length of the bud-emergence period was 3 ± 2 weeks for insect-pollinated species.

Flowering

There were several seasonal trends in flowering patterns during the four-month blooming period at the prairie site. Late-blooming species tended to have heads of small flowers, instead of the large, loosely arrayed flowers prevalent early in the season. Eurasian insect-pollinated species (e.g., *Vicia sativa* and *Hypochaeris radicata*) flowered for longer periods than did native species (e.g., *Ranunculus occidentalis* and *Camassia quamash*). Throughout the flowering period, blooming was staggered both in the insect-pollinated and wind-pollinated species. Six species which initiated blooming between mid-June and early August but do not appear on Figure 2 because they have less than 0.4 percent cover are *Vicia hirsuta, Delphinium nuttallii, Eriophyllum lanatum, Solidago canadensis, Senecio jacobaea,* and *Danthonia californica* (Jackson 1978). Based on data from all species at the site, insect-pollinated species initiated flowering over 95 percent of the total flowering period of four months. Wind-pollinated species initiated flowering during 50 percent of the total flowering period (Fig. 2). Figure 3 contrasts the number of plants in flower and the number of species in flower in the 50 sampling plots during the flowering periods at both sites. In both anemophilous and entomophilous groups at the prairie, the number of species in bloom does not coincide with abundance of plants in flower. There were more entomophilous species

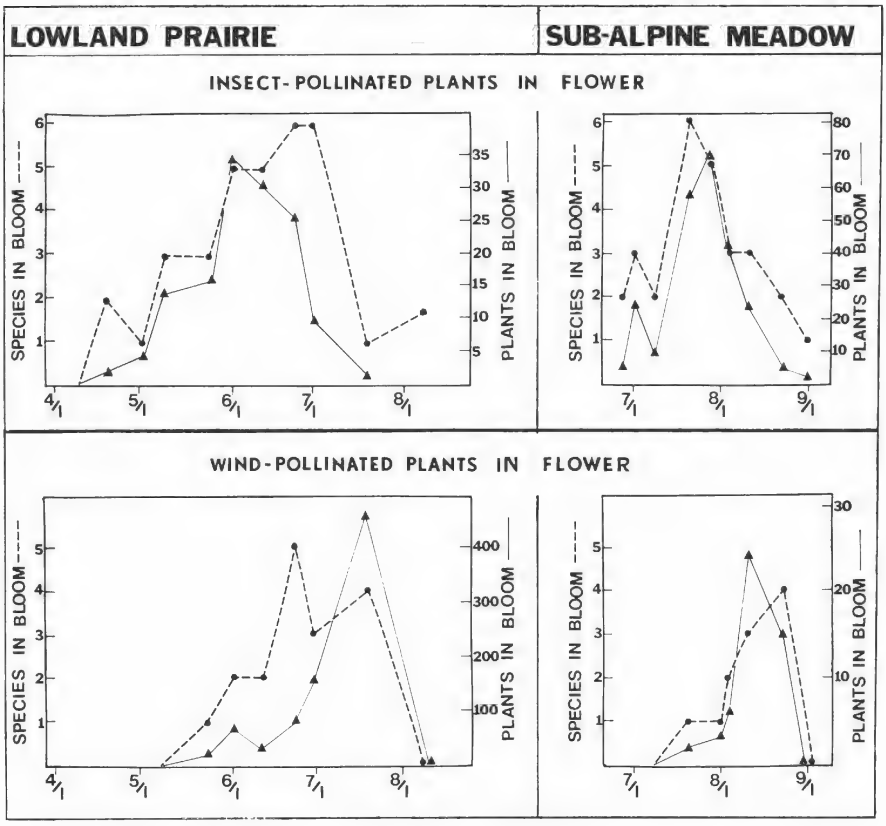


Figure 3. Flowering abundance and species in bloom of insect- and wind-pollinated plants during the flowering periods at prairie and subalpine sites based upon 25 0.1 m^2 plots.

in bloom after peak flowering by individuals, whereas the opposite was observed in the wind-pollinated plants.

Compared to the prairie, much less diversity in flowering characteristics was observed at Grand Park. Dominant insect-pollinated species flowered by early August, while wind-pollinated species bloomed later, completing flowering by late August (Fig 3). In entomophilous species, two types of flowering patterns are recognizable. Early-blooming entomophilous species are abundant, have rosettes of basal leaves and small, compact inflorescences of achene-producing flowers. Later in the season, less abundant, leafy-stemmed, entomophilous species with racemes of larger, capsule-producing flowers began to bloom, e.g., *Lupinus latifolius, Pedicularis contorta*, and *Gentiana calycosa.*

The separation of flowering times among subalpine meadow species was not as pronounced as it was at the prairie. Flowering initiation lasted less than two months as compared with almost four months at the prairie. The entire spectrum of flowering initiation times is shown for Grand Park in Figure 2. Insect-pollinated species initiated flowering during only 55 percent of the flowering period, and initiation of flowering

in wind-pollinated species was staggered over 50 percent of the total flowering period (Fig. 2). In both insect- and wind-pollinated groups in the subalpine meadow, abundance of plants in flower coincided reasonably with the peak of species in bloom (Fig. 3). There was a two week period when five to six entomophilous species were blooming simultaneously at Grand Park, and in no species was flowering completely displaced away from this period of high overlap. Insect-pollinated species that began to bloom after 1 August contributed little to flowering abundance in the community. Three to four of a total of five graminoid species were simultaneously in bloom for two weeks in late August. Only one grass, *Danthonia intermedia* began to bloom after the peak of graminoid flowering abundance.

Seed production

Phenological patterns in seed production closely follow those of flowering at the prairie site. A mean of 5 $\pm$ 4 weeks was spent by the dominant entomophilous species in seed producing stages. No comparable time interval could be calculated for the grasses. Success of seed production varied considerably between species. Species that had a high percentage of floral buds that produced fruits were *Ranunculus occidentalis* (90 percent), *Potentilla gracilis* (90 percent), and *Camassia quamash* (50 percent). Late season buds of *Camassia* dried before flowering in 1977. The percentages were much lower in the leguminous introduced species. Approximately 25 percent of flowers produced fruits in *Vicia sativa* and 10 percent in *Cytisus scoparius*. But in *V. sativa*, 70 percent of the ovules in developing fruits developed into seeds, while seed production in other species did not exceed 45 percent. The estimated number of seeds produced per plant varies greatly within and between species, averaging about 10 in *Vicia sativa*, 80 in *Camassia quamash*, and 120 in *Ranunculus occidentalis*. Clearly, species in this community differ widely in their ovule-bearing capacities as well as in the proportion of ovules which successfully develop into seeds.

Dormancy seemed to be controlled in large part by drought conditions, because many plants were dry before seeds dispersed.

In some subalpine meadow species, fruit formation was observed nearly as soon as flowering began (Fig. 1) and closely paralleled flowering in time. However, the length of the fruit-producing period was usually one to two weeks longer than the flowering period, averaging 4 $\pm$ 1 weeks in the dominant entomophilous species. In *Aster alpigenus, Polygonum bistortoides*, and *Potentilla diversifolia*, for which the quantity of seed production was estimated, approximately half of the floral buds produced fruits, suggesting that seed production success per inflorescence is reasonably similar. Plants also produced nearly the same number of achenes per plant (50-70). Apparently, seed-bearing capacity as well as successful fertilization and development of ovules varies more between prairie species than between subalpine species.

Drying and discoloration of leaves in almost all species began as early as mid-August, during seed and fruit dispersal. The only entomophilous species that retained green leaves until snowfall in mid-September was *Aster alpigenus*. Leaves of wind-pollinated *Carex* and *Trisetum* also remained partially green until snowfall.

Comparison of phenologies by ordination

In a Reciprocal Averaging ordination of peak dates of floral bud emergence, flowering,

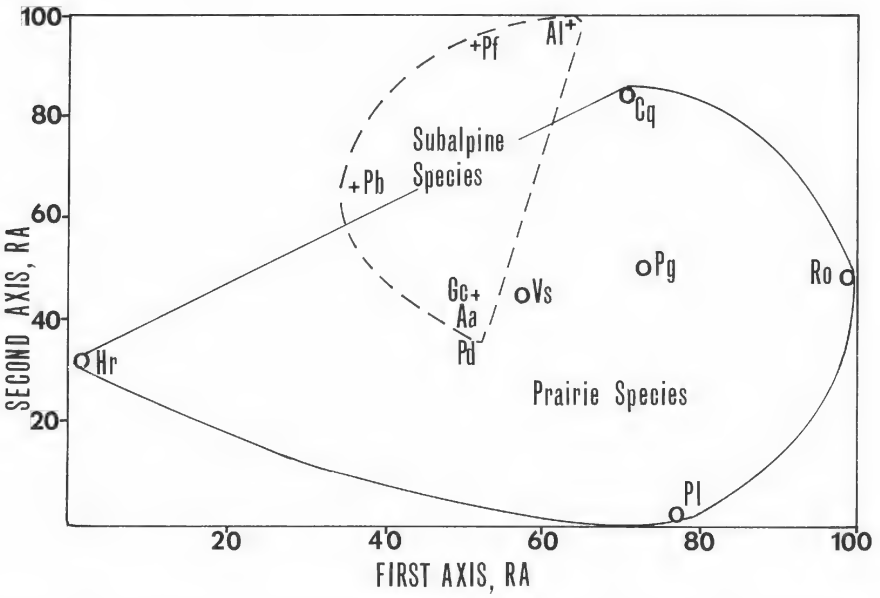


Figure 4. Reciprocal Averaging ordination of peak dates in reproductive periods for the six most abundant entomophilous species at each site. Scatter Creek Prairie species: Cq = *Camassia quamash*, Hr = *Hypochaeris radicata*, Pg = *Potentilla gracilis*, Pl = *Plantago lanceolata*, Ro = *Ranunculus occidentalis*, Vs = *Vicia sativa*. Grand Park species: Aa = *Aster alpigenus*, Al = *Antennaria lanata*, Gc = *Gentiana calycosa*, Pb = *Polygonum bistortoides*, Pd = *Potentilla flabellifolia*.

and fruit production periods of the six most dominant species from both sites, subalpine species group closely together, while those from the lowland prairie are spatially dispersed (Fig. 4). Although no distinct variables can be assigned to the ordination axes, the tightness of the Grand Park species cluster can best be explained by 1) the simultaneous occurrence of developmental events between species; and 2) the short duration and synchrony of developmental stages within species populations at this site. In contrast, at Scatter Creek Prairie, 1) phenology is more separated in time between species; and 2) duration and synchrony of phenological stages within species populations varies greatly between taxa.

Phenology in 1978

At Scatter Creek Prairie, the phenological trends observed in 1977 were repeated in 1978 with two exceptions: 1) some species emerged and produced floral buds two to four weeks earlier (e.g., *Camassia, Potentilla*, and *Anthoxanthum*); and 2) flowering periods of some entomophilous species lasted two weeks longer (e.g., *Camassia, Ranunculus, Potentilla*, and *Vicia sativa*), presumably because water stress did not limit growth so early in the season. However, visits to the site on identical dates in 1977 and 1978 showed that dates of floral bud emergence and peak flowering were the same in both years for most species (e.g., *Ranunculus, Vicia sativa, Senecio, Solidago, Agrostis tenuis, Festuca, Arrhenatherum*, and *Poa*).

At Grand Park, snowmelt was one month later than in the previous year and growth cycles were even more compressed in 1978 than in 1977. Leaf emergence was delayed until early July, yet flowering reached its peak among insect-pollinated species (early August) and in wind-pollinated species (mid-August) at very close to the same time as in the previous year. The duration of flowering was shorter in many species in 1978 than in 1977 (e.g., *Aster alpigenus, Potentilla diversifolia, Antennaria lanata*). By 1 October 1978, following warm fall weather conditions, winter snows had not begun. Despite the lack of snow cover, dormancy was well-advanced in all meadow species. Only a few species had any green leaves; these were graminoids and occasional individuals of *Tauschia stricklandii.*

Pollination Biology

At the prairie site, insect pollinator diversity and abundance were at their heights from late May to mid-June, coinciding with the peak of flowering in the community. Twice as many insect species were present during this interval as before or after (8 *vs.* 3-5 species), and pollinators were also approximately twice as abundant. Approximately 40 individuals were observed per six-hour visit at the flowering peak *vs.* 10-20 earlier or later in the season.

Specialist insect visitors were found seasonally on the native species *Camassia quamash* and *Ranunculus occidentalis.* Specialists were often more abundant than generalists but were absent after early June. One species of anthomyid fly visited only buttercups. The butterfly *Euphydryas editha* (Nymphalidae), an empidid fly, and an anthophorid bee visited only camas flowers. Two bee species (Halictidae, Andreninae) and one fly species (Bibionidae) were "semi-specialists" that were found on two native species (*R. occidentalis* and either *C. quamash* or *Potentilla gracilis*). No plant species was visited by only one specialist pollinator species. Generalists such as *Bombus* spp., *Coenonympha tullia* (Satyridae) and Skippers (Hesperidae) were seen commonly on both native and alien plant species. However, few insect visitors were observed on the numerous flowers of the alien species *Vicia sativa* and *Cytisus scoparius*, especially during the flowering periods of *Ranunculus* and *Camassia. Apis mellifera* was seen rarely on *Hypochaeris radicata.* Of these 10 pollinator taxa, half are specialists and semi-specialists, and half are generalists. In addition, single sightings were made of eight hymenopteran and dipteran taxa and two lepidopterans mainly on buttercups, camas, and *Potentilla*, but also on late-blooming *Hypochaeris* and *Senecio.*

At Grand Park, pollinator diversity and abundance were highest at the peak of flowering, as at the prairie site. However, abundance of insects was greater during and after the flowering peak at Grand Park than at the prairie. For a three-week period (mid-July to early August), insect pollinators were extremely numerous at Grand Park, coinciding with peak flowering of early-blooming, dominant species. In early July, fewer than five individuals of only two pollinator species were observed per field visit. By mid-July, more than 40 visits by at least eight species were recorded, and in late July nearly 100 visits by 10 species were noted in six-hour periods. Flowering abundance dropped sharply in early August (Fig. 3), but many insects of pollinator taxa (approximately 30 individuals in four species) remained at the site in flight or resting on leaves, despite the lack of flowers. Late August brought complete cessation of pollinator activity with the exception of a few visits to gentians by *Bombus* spp; however, a few syrphids were still seen in flight.

In contrast to the prairie, few specialist pollinators were observed at the subalpine site. By far the most abundant pollinators in the Grand Park meadow were syrphid flies that were the principal pollinators of all early-blooming species (aster, bistort, *Potentilla* sp., and *Antennaria*). These flies were generalist pollinators with no clear species preference and often visited a series of flowering species. *Serricomyia, Eristalis,* were present from July to September while collections of *Syrphus, Metasyrphus*, and *Melanostoma* were made only before 1 August. Only one abundant insect, *Boloria titania* (Nymphalidae), was identified as a specialist; it had a strict association with *Aster alpigenus* during the entire flowering season. Tenthredinid wasp species were found rarely on the *Potentilla* species and *Lupinus. Bombus* spp. visited *Aster* and occasionally *Polygonum*, but were by far the most important visitors to the infrequent, late-blooming species *Lupinus, Pedicularis*, and *Gentiana.*

Discussion

Life Form Diversity and Phenology

Raunkiaer (1934) showed that the height of perennating buds reflects plant adaptation to climate and that certain life forms are characteristic of certain climatic regimes. High life form diversity within a structurally homogeneous community such as Scatter Creek Prairie could be a result of temporal variability in environmental conditions. The mild, maritime, summer dry climate of the Puget Sound Lowland may also be important in allowing species of diverse life forms to coexist. In contrast, the short harsh growing season of the subalpine meadow limits the number of successful life forms. I suggest that life form diversity in these meadow communities is controlled by (1) climatic severity, and (2) the amount of temporal variability in environmental conditions during the growing season.

At least seven phenological patterns can be recognized in the species of the lowland prairie. These incluude: (1) summer dormant herbs that grow slowly all winter, flowering and dispersing seed simultaneously with early summer dormancy (*Vicia sativa* and *Ranunculus occidentalis*; (2) rosette plants that are active year-round (*Hypochaeris radicata* and *Plantago lanceolata*; (3) geophytes with a short period of growth and flowering in the spring (*Camassia quamash* and *Delphinium nuttallii*); (4) annuals that germinate in winter and complete growth by early summer (*Aira pracecox* and *Vicia hirsuta*; (5) larger herbs with thickened rootstocks that sprout late in the spring and flower in late summer (*Solidago canadensis* and *Eriophyllum lanatum*); (6) a winter deciduous shrub, tolerant of summer moisture stress (*Cytisus scoparius*); and (7) grasses that flower in midsummer following a long period of vegetative growth and undergo drought-induced dormancy soon after fruit production (*Agrostis tenuis*). Among all species there is a general trend towards having a long period of vegetative growth before flowering and seed dispersal simultaneous with drought-induced dormancy. Grasses are the dominant species in the prairie community and they best express this growth pattern.

Three basic patterns of seasonal growth were observed in the subalpine meadow community. Dominant species such as *Aster alpigenus, Polygonum bistortoides, Potentilla flabellifolia*, and *Antennaria lanata* sprout just after snowmelt, reach maximum size early in the summer, flower (if at all) early in the season, and become dormant while conditions still appear well-suited for growth. Dormancy may be induced photoperi-

odically in preparation for the unpredictable arrival of winter snowcover. The graminoids have a slightly longer vegetative growth period, flower over a shorter period, and retain green leaves longer. A small group of infrequent species (*Pedicularis contorta, Lupinus latifolius*, and *Gentiana calycosa*) flower later in the season.

Changing environmental resources at the prairie site, especially of moisture and temperature during the long growing season, enable plants with differing growth requirements to survive here. For example, annuals, fibrous-rooted forbs, and rhizomatous grasses grow slowly for long periods under cool moist conditions. Geophytes grow rapidly for short periods when moisture is high and temperatures rise in spring. Hemicryptophytes with thickened rootstocks that break dormancy in spring have higher tolerances for summer moisture stress. In the subalpine, a shortage of time prevents the coexistence of plants with strikingly different growth periods.

Pollination Biology

The staggered short-term appearances of a number of specialist and semi-specialist pollinators at Scatter Creek Prairie suggest a long history of coevolution with native entomophilous species. Apparently, the separation in time of flowering in plant species with different life forms must be predictable enough to support ephemeral pollinators with narrow preferences. Alien species with flowering periods longer than any native species (e.g., *Vicia sativa* and *Hypochaeris radicata*) cause greater flowering overlap in the community. Generalist pollinators may be more successful when flowering overlap is high; however, the proportion of seed set in the alien species pollinated by generalists at the prairie is low. This observation suggests that pollination failure may be occurring. Similarly, Parrish and Bazzaz (1979) found that there was little separation in seasonal flowering and fewer specialist insect pollinators in early successional annual communities in Illinois, but that in a late successional tall-grass prairie, flowering periods were shorter, flowering peaks were offset, and there were relatively more specialist pollinators.

In the subalpine meadow, flowering overlap in the community was high and almost all pollinators are generalists. Specialization may be a risk to both plants and insects when the onset of a short season is extremely variable. Because many species bloom simultaneously in the subalpine meadow, generalist pollinators would always be assured of some success. There are two ways in which these subalpine plant species may be adapted to maximize pollination success by generalists: (1) duration of flowering of each plant is prolonged in the achene-producing flowers present in the dominant species, hence increasing the probability of successful pollination; and (2) species of similar growth form (*Aster alpigenus, Potentilla* spp., and *Polygonum bistortoides*) have somewhat offset flowering periods, decreasing flowering overlap, especially at the beginning of the flowering period.

Natives and Aliens

Since there has been more than 30 years with no grazing disturbance, plant growth patterns at Scatter Creek Prairie presumably reflect community degradation and community instability less than they reflect environmental conditions during the growing season. Several characteristics distinguish native from alien species at Scatter Creek Prairie. All native species are hemicryptophytes or cryptophytes. Although grasses, winter-active forbs, and summer-active forbs are represented by both native and alien species, annual,

shrub, and perennially green rosette plants are all aliens. Geophytic species, which are all native, were probably more numerous before invasion by Eurasian species (del Moral and Deardorff 1976). While some native species of other life forms could have been eliminated by competition from the introduced species, perhaps disturbance has resulted in a greater diversity of life forms than would have been present in a community of natives. Temporal variability in environmental conditions during the long prairie growing season provides many niches, allowing a wide variety of aliens to survive successfully. In the subalpine meadow, stringent environmental demands prevent alien species from invading the community.

Acknowledgments

This study was partially supported by a Sigma Xi Grant-in-Aid of Research. I thank Lawrence C. Bliss and Daniel Mann for reading the manuscript. Roger del Moral provided encouragement during the study. I appreciate the help of Virginia Adams with field work and that of Mark Deyrup with identification of insects.

Literature Cited

Al-Mufti, M. M., C. L. Sydes, S. B. Furness, J. P. Grime, and S. R. Band. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. J. Ecol. 65:759-791.
Bliss, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. Ecol. Monogr. 26:303-337.
Borror, D. J., D. M. Delong, and C. A. Triplehorn. 1976. An Introduction to the Study of the Insects. Holt, Rhinehart and Winston, New York.
del Moral, R., and D. C. Deardorff. 1976. Vegetation of the Mima Mounds, Washington state. Ecol. 57:520-530.
Heinrich, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. Ecol. 57:890-899.
Henderson, J. A. 1974. Composition, distribution and succession in subalpine meadows in Mt. Rainier National Park, Washington. Oregon State Univ. Corvallis, Ph.D. thesis.
Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61:237-249.
Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Wash. Press, Seattle.
Holway, J. G., and R. T. Ward. 1965. Phenology of alpine plants in northern Colorado. Ecol. 46: 73-83.
Jackson, L. E. 1978. Life cycles of plants in two western Washington meadow communities. Univ. of Washington, Seattle, M.S. thesis.
Johnson, D. A., and M. M. Caldwell. 1974. Field measurements of photosynthesis and leaf growth rates of three alpine plant species. Arctic and Alpine Res. 6:245-251.
Monasterio, M., and G. Sarmiento. 1976. Phenological strategies of plant species in the tropical savanna and the semi-deciduous forest of the Venezuelan Llanos. J. Biogeography 3:325-356.
Mooney, H. A., and C. Chu. 1974. Seasonal carbon allocation in *Heteromeles arbutifolia*, a California evergreen shrub. Oecologia 14:295-306.
Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. Oikos 22:398-402.
Parrish, J. A. D., and F. A. Bazzaz. 1979. Difference in pollination niche relationships in early and late successional plant communities. Ecol. 60:597-610.
Pemadasa, M. A., and P. H. Lovell. 1974. Factors controlling the flowering time of some dune annuals. J. Ecol. 62:869-880.
Pitt, M. D., and H. F. Heady. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. Ecol. 59:336-350.
Pyle, R. W. 1974. Watching Washington Butterflies. Natl. Audubon Soc., Seattle.
Raunkiaer, C. 1934. The Life Forms of Plants and Statistical Geography. Oxford Univ. Press, Oxford. Reprinted by Arno Press, New York. 1977.
Reader, R. J. 1975. Competitive relationships of some bog ericads for major insect pollinators. Canad. J. Bot. 53:1300-1305.
Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Science 147:250-260.

Received February 24, 1981
Accepted for publication May 4, 1981

Charles J. Henny

U.S. Fish and Wildlife Service
480 SW Airport Road
Corvallis, Oregon 97330

Chris Maser

Bureau of Land Management
Route 2, Box 2315
La Grande, Oregon 97850

John O. Whitaker, Jr.

Department of Life Sciences
Indiana State University
Terre Haute, Indiana 47809

and

T. Earl Kaiser

U.S. Fish and Wildlife Service
Laurel, Maryland 20811

Organochlorine Residues in Bats after a Forest Spraying with DDT

Abstract

Background levels of DDT and its metabolites (ΣDDT) were extremely low or not detected in five species of forest-dwelling bats in northeastern Oregon, i.e., areas not sprayed with DDT in 1974. Other organochlorine pesticides were rarely found and no polychlorinated biphenyls (PCBs) were detected at any time during the study. Four of five species of bats showed significant changes in ΣDDT residues in their carcasses following the single DDT spray application. *Myotis californicus* and *M. volans* showed the highest postspray carcass residues, 6.90 and 6.21 ppm (wet weight). respectively. *Lasionycteris noctivagans* and *Eptesicus fuscus* also showed an increase; however, *M. evotis* exhibited no significant postspray change. By 1977 (3 years postspray), residues declined and only *M. californicus* and *M. volans* contained levels that were significantly above those in the nonspray (control) area. We are uncertain if the elevated residue levels resulting from the DDT spray project adversely affected any of the bats. An attempt to relate bat carcass ΣDDT residues to food habits, through analysis of stomach contents, yielded no clear relationships.

Introduction

Several studies have related bat population declines to insecticides (e.g., Geluso *et al.* 1976, Findley 1973, Mohr 1972, Stebbings 1970), including a study of the endangered gray bat (*Myotis grisescens*) (Clark *et al.* 1978). Some surveys of organochlorine residues in free-living bats have been conducted (Jefferies 1972, Dunsmore *et al.* 1974, Clark *et al.* 1975, Reidinger 1976, Clark and Prouty 1976), but the residues resulting from an operational forest spray project with DDT for insect control have never been measured in nontarget free-living bats. We have evaluated the impact of one DDT spray project on residues in five species of forest-dwelling bats and have attempted to relate relative contamination within particular bats to their food habits.

Our study explored residue patterns in bats following a DDT spray project in

northeastern Oregon, eastern Washington, and northern Idaho. Between 9 June and 25 July 1974, 172,620 ha of coniferous forest were aerially sprayed with DDT in an effort to control larvae of the Douglas-fir tussock moth (*Orgyia pseudotsugata*). The majority of the acreage (170,348 ha) was treated at the calculated rate of 0.84 kg DDT/ha mixed in 3.8 l of fuel oil (Graham *et al.* 1975).

In addition to measuring residue concentrations in carcasses, stomach contents were analyzed to study food habits that, in turn, may lead to a better understanding of the residue concentrations.

Methods and Materials

We collected five species of bats in mist nets on 12 and 13 August in 1975, 1976, and 1977. Controls were collected outside the spray area in eastern Oregon during the same three-year period. Because of logistics (having to find and secure control specimens as far from the spray area as possible) control bats could not be captured on the same dates as those collected in the spray area. Collection dates for the control bats, however, were within one month of the spray area collections.

Bats from the spray area were collected at two livestock ponds: (1) Rockwall Spring, 18.4 km NNE of Wallowa (T3N, R43E, SW¼, NW¼ Sec. 14), and (2) Powwatka Ridge (T3N, R43E, NE¼, SW¼ Sec. 21). Wallowa County is in the Blue Mountains physiographic province of northeastern Oregon, and the ponds are in the ponderosa pine (*Pinus ponderosa*) zone (Franklin and Dyrness 1973). The ponds are basically in a mixed coniferous forest that abuts an open meadow. Rockwell Spring is a stock pond within the forest edge, mainly old-growth ponderosa pine, western larch (*Larix occidentalis*), and lodgepole pine (*Pinus contorta*). The stock pond on Powwatka Ridge is surrounded on two sides by a forest of large ponderosa pine, western larch, Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and a stand of quaking aspen (*Populus tremuloides*). The other two sides border an open meadow.

The percentage of sprayed area surrounding the ponds was as follows: (1) 1.6 km radius—65 percent, (2) 3.2 km radius—60 percent, (3) 4.8 km radius—60 percent, (4) 6.4 km radius—50 percent, and (5) 8 km radius—45 percent. Much of the unsprayed area consisted of canyon slopes. Although the home ranges of these bats were not known, we assumed that, because they were mainly forest dwellers in the Blue Mountains (Thomas 1979), they fed within the sprayed forested area most or all of the time. *M. evotis* showed an affinity for large ponderosa pines, whereas *M. volans* was often the most abundant species in the large, dense stands of mature grand fir. *M. californicus*, a species associated with open stands, was not abundant anywhere. *L. noctivagans* and *E. fuscus* were widely distributed but were seldom netted in large numbers (Maser, unpubl. data).

Of the five species, *L. noctivagans* was the only solitary form, and also the only one known to migrate out of state (Barbour and Davis 1969); migratory information about the study area population is not available. Thomas (1979) suggested that, within the study area, the other species were colonial and resident; they used hollow trees and snags and loose slabs of bark as sites for roosting, rearing young, and hibernation. No human habitations were available to the bats in the area.

All specimens were placed in aluminum foil and frozen immediately. Specimens were later thawed and weighed. Heads were severed at the base of the skull, and brains were

removed and weighed. Skulls were dried, cleaned, and deposited in the Puget Sound Museum of Natural History, University of Puget Sound, Tacoma, Washington. The stomach and gastrointestinal contents were removed. That part of the body remaining, including the gastrointestinal tract, was analyzed as "carcass." Stomach contents were preserved in 10 percent formalin. They were later examined and identified by comparison with an insect reference collection. We made visual estimates of the percentage volume of each food in each stomach with a 10- to 70-power zoom dissecting microscope. The technique has been thoroughly discussed by Whitaker (1972).

Samples were analyzed for organochlorine contaminants at the Patuxent Wildlife Research Center, Laurel, Maryland. The ground samples were thoroughly mixed with anhydrous sodium sulfate to remove moisture. All samples were then extracted for 7 hours with hexane in a Soxhlet apparatus. Lipids were separated from organochlorine compounds by Florisil column chromatography (Cromartie *et al.* 1975). We separated the organochlorine pesticides and PCBs on a SilicAR^{R} column into three fractions and then quantified them with a gas-liquid chromatograph (GLC) using an electron-capture detector and a 1.5 percent OV-17/1.95 percent QF-1 column. Residues in 2 percent of the samples were confirmed with a combined gas-liquid chromatograph/mass spectrometer (GLC/MS). Operating conditions for the GLC and the GLC/MS have been published (Cromartie *et al.* 1975, Kaiser *et al.* 1980).

Samples were analyzed for DDE, DDD, DDT, dieldrin, heptachlor epoxide, oxychlordane, *cis*-chlordane, *trans*-nonachlor, *cis*-nonachlor, endrin, toxaphene, HCB, mirex, and PCBs. The testing procedure for measuring pesticide recovery involved spiking tissues of mallard (*Anas platyrhynchos*) with standard organochlorine compounds. The average recoveries ranged from 80 to 104 percent. Residue levels on a wet weight basis were not corrected for percentage recovery. The lower limits of quantifiable residues for pesticides and PCBs were 0.5 and 2.5 ppm in the brain, and 0.1 and 0.5 ppm in the carcass, respectively.

Because the residue data were positively skewed, they were log transformed for all statistical testing, and expressed as geometric means. Residue levels of ΣDDT (DDT, DDE, DDD) in carcasses reported as "not detected" (ND) entered the computation as 0.05 (half the value of the detection limit 0.1). A two-way analysis of variance for $\log_{10}$ (ΣDDT) carcass residues for the five species and groups (Control, 1975, 1976, 1977) showed a significant interaction ($P < 0.001$). This result implies that the "response" of each species was different and, similarly, that the "order" of the species differs among groups. Multiple comparisons using the Bonferroni method (Neter and Wasserman 1974) were done, using the means for each species-group category.

Results

ΣDDT Residues in Bat Carcasses

The most abundant individuals per species for any given year were *M. volans* and *M. evotis* in 1975. These data were used to test if sex significantly influences ΣDDT residues. The geometric mean for 10 male *M. volans* was 6.31 ppm, whereas for nine females it was 6.11 ppm. Eleven of the 20 *M. evotis* contained no detectable levels of DDT or its metabolites; 10 males had a geometric mean of 0.10 ppm and 10 females, 0.07 ppm. The log transformed data yielded no significant differences between means

for either *M. volans* ($t = 0.15$ NS), or *M. evotis* ($t = 1.28$ NS); thus, sexes were pooled.

Comparisons of residues of DDT and its metabolites in the carcasses of 142 bats are shown in Table 1. Overall residues were low or not detectable in the controls; when present, however, the residues were almost entirely the metabolite DDE. A matrix showing multiple comparisons of the ΣDDT mean carcass residues relating time after spray to each bat species is shown in Table 2. After the spray, the ΣDDT residues increased in *M. californicus, M. volans*, and *E. fuscus*, and were significantly different ($P < 0.05$) in 1975 than in the controls; and by 1976 *L. noctivagans* residues had increased to a point where they were also significantly different from the controls. A general residue decline occurred by 1977, and *L. noctivagans, E. fuscus*, and *M. evotis*

TABLE 1. Residues of DDT and its metabolites in five species of bats following a DDT application (carcass, ppm wet weight).

Category (n)	Geometric mean (range)			
	DDE	DDT	DDD	ΣDDT
M. californicus				
Control (3♂, 3♀)	a			a
1975 (5♂)	4.58 (2.9-9.3)	1.96 (1.4-3.2)	0.31 (0.22-0.44)	6.90 (4.8-13)
1976 (2♂)	1.85 (1.8-1.9)	0.34 (0.22-0.52)	0.22 (0.19-0.26)	2.44 (2.3-2.6)
1977 (5♂, 1♀)	0.68 (0.26-1.0)	a		0.80 (0.36-1.2)
M. volans				
Control (4♂, 3♀)	0.39 (0.17-0.88)			0.50 (0.27-0.98)
1975 (10♂, 9♀)	5.42 (1.8-10)	0.41 (0.16-0.85)	0.26 (ND-0.50)	6.21 (2.0-11)
1976 (1♂, 3♀)	3.66 (1.7-4.9)	0.12 (ND-0.50)	0.13 (ND-0.27)	3.96 (1.8-5.3)
1977 (2♂, 4♀)	0.96 (0.16-3.5)	0.11 (ND-0.27)		1.17 (0.26-3.8)
L. noctivagens				
Control (3♂, 5♀)	0.61 (ND-1.5)	b	a	0.80 (ND-1.8)
1975 (3♂)	1.50 (1.5)	0.78 (0.77-0.78)	0.20 (0.15-0.26)	2.48 (2.4-2.5)
1976 (3♂, 1♀)	2.18 (0.87-4.5)	0.35 (ND-0.93)	0.48 (0.24-1.1)	3.08 (1.2-6.5)
1977 (8♂)	0.92 (0.36-2.0)	0.23 (0.12-0.52)	b	1.22 (0.56-2.7)
E. fuscus				
Control (3♂, 3♀)	0.33 (0.21-0.82)			0.43 (0.31-0.92)
1975 (3♂)	1.63 (1.4-2.2)	0.18 (ND-0.48)	a	1.93 (1.5-2.8)
1976 (3♂)	0.65 (0.27-1.0)	0.09 (ND-0.14)	a	0.86 (0.46-1.2)
1977 (10♂, 3♀)	0.40 (ND-2.4)	0.10 (ND-0.37)		0.58 (ND-2.7)
M. evotis				
Control (3♂, 3♀)				ND
1975 (10♂, 10♀)	b	c	d	0.20 (ND-0.40)
1976 (3♂, 3♀)	0.16 (ND-0.44)	d		0.30 (0.23-0.64)
1977 (4♂, 4♀)	0.14 (ND-0.35)	a		0.26 (ND-0.50)

[a]Present at low levels in one individual.

[b]Present at low levels in three individuals.

[c]Present at low levels in two individuals.

[d]Present at low levels in five individuals.

TABLE 2. Multiple comparisons of the ΣDDT mean carcass residues relating time after spray to each bat species (read horizontally).

Species	Control	1975	1976	1977
M. californicus	A	B	BC	C
M. volans	A	B	B	C
L. noctivagans	A	AB	B	AB
E. fuscus	A	B	AB	A
M. evotis	A	A	A	A

Note: The sharing of a letter indicates no significant difference ($P > 0.05$) among years for a given species.

residues did not differ significantly from the controls, although *M. evotis* never attained levels significantly different from controls. The parent material (DDT) that was prominant the first year postspray was seldom detected during the last year of the study. The contrasts in residues among the five bat species are particularly noteworthy because the bats were annually collected at the same site on the same dates.

Deposition of fat in late summer is common among bats (e.g., Jefferies 1972); therefore, in an attempt to collect bats at the same stage of their lipid cycle, all bats were collected in the spray area during a two-day period. Nevertheless, species-specific differences in lipid cycles still could be responsible for either diluting or concentrating carcass residues in some species (Table 3). The ΣDDT residues in carcasses do not directly or inversely follow the species ranking based on lipid content (Table 1). Thus, the residues reported are not an artifact of the different lipid values reported among the species.

TABLE 3. Percentage lipid in the carcasses of bats collected in the DDT spray area during the three-year study.

Species	n	Mean±SE	Range
M. volans	29	4.27±0.27	2.1-9.2
M. californicus	13	6.34±0.78	2.6-10.0
M. evotis	34	6.92±0.41	2.8-12.2
L. noctivagans	14	10.86±1.04	3.6-16.2
E. fuscus	19	17.36±2.06	3.6-33.5

Other Residues in Bat Carcasses

With the exception of DDT and its metabolites, the bats in this study contained few organochlorine pollutants. In fact, *E. fuscus* and *M. californicus* contained no other organochlorine pollutants at detectable levels. Several *M. volans* carcasses contained other organochlorines: heptachlor epoxide (0.10, 0.11, and 0.13 ppm), oxychlordane (0.18 and 0.18 ppm), dieldrin (0.17 ppm), and *trans*-nonachlor (0.16 ppm). One *L. noctivagans* contained 0.44 ppm *trans*-nonachlor, and one *M. evotis* contained 0.24 ppm *trans*-nonachlor. PCBs were not detected in any of these forest-dwelling bats.

Residues in Bat Brains

Residues of DDE in bat brains may be expected to vary in relation to the ratio of DDE to lipid in the entire animal (Clark and Prouty 1976). Residues were detected in only one brain ($\geqq$ 0.5 ppm) of the three species (*M. evotis, E. fuscus, L. noctivagans*) which contained the lowest carcass residues (45 brains analyzed with paired sets of carcasses). An *M. evotis* brain contained 0.67 ppm DDE (wet weight). The highest residue of ΣDDT on a lipid basis in an individual carcass of each of these species was: *M. evotis*, 9.7 ppm; *E. fuscus*, 35 ppm; and *L. noctivagans*, 85 ppm. The relation between DDE residues in brain and those in carcass lipids of *M. californicus* could not be measured because the extremely small size of the brain raised the limit of detection above 0.5 ppm; however, the highest brain residue recorded for the species was 3.6 ppm DDE (wet weight). The *M. volans* relation is shown in Figure 1 for 21 paired sets of data with the highest DDE brain residue being 2.3 ppm.

Residues began appearing in *M. volans* brains when levels in the carcass (lipid basis) approached 100 ppm. In agreement with this finding is that only one brain of

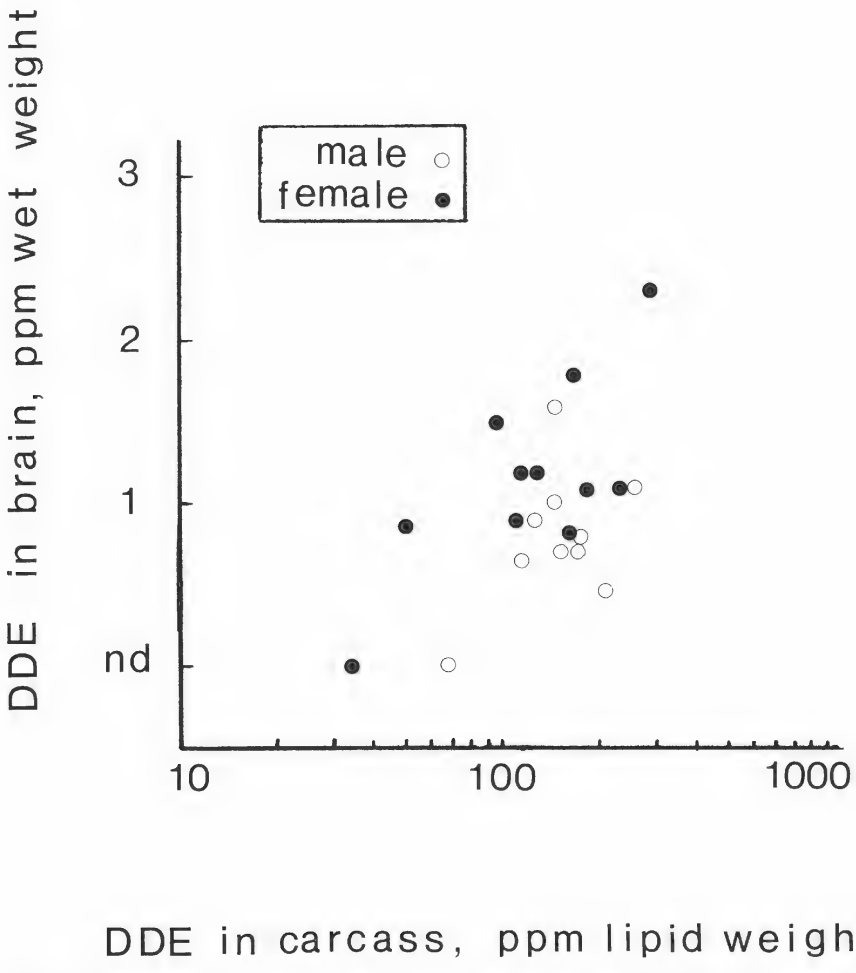


Figure 1. Relationship of DDE residues in brain (wet weight basis) to those in carcass (lipid weight basis) of *Myotis volans*.

the other three species contained detectable limits of DDE, and none of the 45 individuals contained residues in their carcasses above 85 ppm. Our brain-carcass findings are in agreement with those of Clark and Prouty (1976).

Food Habits of Bats

Since bats presumably obtain DDT from their food, and since the insects eaten vary among bat species (e.g., Whitaker *et al.* 1977), we hoped to relate ΣDDT levels in the bats to their food habits. Although the food habits of the five species of bats did vary (Table 4), several factors may contribute to a weakened relationship between ΣDDT in bat carcasses and food habits. For example, grouping of prey species by insect Order may not provide the required resolution to clearly demonstrate such a relationship. Further, the limited period of bat collection in this study may only reflect the

bat food habits at that particular time. In an attempt to remedy the latter situation, food habits of the same species of bats from western Oregon (Whitaker *et al.* 1977) were compared with the data from our study. Whitaker's bats were collected over a four and one-half year period. The food habits data from the two studies show similarities but also some differences and suggest that bats are probably opportunistic feeders. Unfortunately, species with opportunistic feeding habits require large collections over time to adequately measure annual prey usage patterns.

TABLE 4. Percentage volumes of major food categories of captured bats from this study and Whitaker et al. (1977). Bat species are arranged in order of ΣDDT burdens (from highest to lowest) and prey in order of overall importance to all species.

Prey (Orders)	M. californicus n=11 (31)[a]	M. volans n=67 (25)	L. noctivagans n=18 (15)	E. fuscus n=13 (30)	M. evotis n=93 (13)
Lepidoptera	73.2 (14.4)	47.7 (78.2)	8.6 (32.0)	16.9 (21.3)	50.4 (46.2)
Diptera	18.3 (60.2)	9.9 (1.6)	1.8 (18.9)	1.9 (15.9)	7.4 (12.3)
Coleoptera	4.1 (0.3)	10.6	3.4 (2.7)	20.3 (34.4)	21.2 (18.0)
Hymenoptera	(0.6)	0.5	25.3 (7.0)	42.3 (5.5)	2.1 (4.2)
Homoptera	(0.6)	21.0 (1.8)	49.9 (3.4)	5.6 (1.5)	6.2 (1.2)
Hemiptera	4.5 (1.6)	6.9 (1.6)	8.6 (6.6)	12.6 (1.6)	4.8 (3.8)
Isoptera	(4.8)	(7.6)	(14.0)	(12.7)	0.1(3.1)
Arachnida	(7.3)	(4.8)	(1.4)	(2.8)	2.1 (9.6)
Orthoptera	(1.1)	(4.0)	(3.8)	(2.3)	0.2
Trichoptera	(4.7)		(2.7)		
Neuroptera			0.3 (0.3)	0.4	2.3
Unknown	(4.2)	3.2 (0.4)	2.2 (7.0)	(1.8)	3.1 (1.5)
	Mean carcass residues in bats (from TABLE 1)				
A. ΣDDT (ppm peak)	6.9	6.2	3.1	1.9	0.3
B. Controls (ppm)	0.1	0.5	0.8	0.4	0.1
A-B (difference)	6.8	5.7	2.3	1.5	0.2

[a]n = number of stomachs analyzed, values in ( ) from Whitaker et al. (1977).

Discussion and Conclusions

Residue concentrations in bat carcasses following DDT application varied among the five species studied, and the period required for the bats to return to prespray (background) residue levels also differed among species. No clear relation could be established, however, between ΣDDT residue levels in carcasses and a particular Order of prey used by the bats. But, as mentioned earlier, the grouping of prey species by Order may not provide the refinement needed to interpret the residue data.

Because feeding times, heights, and habitats vary among bat species (Kunz 1973), insects belonging to different families are probably eaten. The potential for DDT to concentrate in aquatic systems, however, seems to be greater than in terrestrial systems (Edwards 1970); thus, bats feeding on insects with aquatic life stages may be the most contaminated. Deer and Zabik (1972) reported that midges (Diptera) had a DDE bio-accumulation factor of about 14,000 to 20,000 times over that present in water. They concluded that when this type of magnification is coupled with the consumption of midges, there will be a significant transfer of this biologically active compound to higher trophic levels (for example, *M. californicus* in Table 4).

We conclude that food habits studies of bats will have to be done in more detail and over a longer period of time before correlations between food items and body burdens can be established. Our carcass residue-food habits interpretation could also be

confounded by species-specific differences in organochlorine retention. Controlled laboratory studies would be needed to elucidate organochlorine retention among species.

In another study of insectivorous shrews (primarily *Sorex vagrans*) associated with the same spray project, Herman and Bulger (1979) presented geometric means of carcass residues (ΣDDT) on a wet weight basis as follows: 1974 before spray, 0.56 ppm; 1974 after spray, 8.4 ppm; 1975, 2.4 ppm; and 1976, 1.2 ppm. Peak residues in shrews were reported following the spray in the same year (1974) as the treatment; unfortunately, in our study, the first collection was made in 1975 (one year after spraying). Thus, it seems possible that the period of peak residues in the bats was missed. It should be recognized here that two bat species (*M. californicus* and *M. volans*) in 1975 (Table 1) show more than twice the 1975 shrew residue levels.

Finally, Geluso *et al.* (1976) netted a reference group of 13 young *Tadarida brasiliensis* at Carlsbad Caverns on 19 August 1974. Carcass residues on a wet weight basis of DDE in "younger animals" showed a median of 92 ppm (range 50-300), and in "older animals" a median of 22 ppm (range 13-66). In their study, organochlorine residues in young reached the brain and caused symptoms of poisoning after the mobilization took place during simulated migratory flight. They believed that the reported residues present a serious threat to the bats. There was nothing in the literature to indicate that the lower residue levels found in our study were harmful, although residues may have been much higher during the 1974 postspray period. Any conclusions about the impact of the DDT on bats must therefore be tempered by the fact that critical residue levels in carcasses have not been established.

Acknowledgments

The manuscript was improved by the comments of Eugene H. Dustman and Donald R. Clark, Jr. Christine Bunck assisted with the statistical analysis.

Literature Cited

Barbour, R. W., and W. H. Davis. 1969. Bats of America. Univ. Press Kentucky, Lexington.

Clark, D. R., Jr., and R. M. Prouty. 1976. Organochlorine residues in three bat species from four localities in Maryland and West Virginia, 1973. Pestic. Monit. J. 10: 44-53.

———, R. K. LaVal, and D. M. Swineford. 1978. Dieldrin-induced mortality in an endangered species, the gray bat (*Myotis grisescens*). Science 199: 1357-1359.

———, C. O. Martin, and D. M. Swineford. 1975. Organochlorine insecticide residues in the free-tailed bat (*Tadarida brasiliensis*) at Bracken Cave, Texas. J. Mamm. 56: 429-443.

Cromartie, E., *et al.* 1975. Residues of organochlorine pesticides and polychlorinated biphenyls and autopsy data for bald eagles, 1971-72. Pestic. Monit. J. 9: 11-14.

Derr, S. K., and M. J. Zabik. 1972. Biologically active compounds in the aquatic environment: the uptake and distribution of [1,1-dichloro-2,2,bis (p-chlorophenyl) ethylene], DDE by *Chironomus tentans* Fabricius (Diptera: Chironomidae). Trans. Am. Fish. Soc. 101: 323-329.

Dunsmore, J. D., L. S. Hall, and K. H. Kottek. 1974. DDT in the bent-winged bat in Australia. Search 5: 110-111.

Edwards, C. A. 1970. Persistent Pesticides in the Environment. Chemical Rubber Co., Cleveland, Oh.

Findley, J. S. 1973. The status of southwestern bat populations. Pp. 12-17 *in* Symposium on Rare and Endangered Wildlife of the Southwestern United States. New Mexico Dept. Game and Fish, Santa Fe.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington, USDA For. Serv. Gen. Tech. Rep. PNW-8.

Geluso, K. N., J. S. Altenbach, and D. E. Wilson. 1976. Bat mortality: pesticide poisoning and migratory stress. Science 194: 184-186.

Graham, D. A., J. Mounts, and D. Almas. 1975. 1974 Cooperative Douglas-fir Tussock Moth Control Project, Oregon, Washington, Idaho. USDA For. Serv. Pac NW Reg., Portland, Oregon.

Herman, S. G., and J. B. Bulger. 1979. Effects of a forest application of DDT on nontarget organisms. Wildl. Monogr. 69.

Jefferies, D. J. 1972. Organochlorine insecticide residues in British bats and their significance. J. Zool. 166: 245-263.
Kaiser, T. E., *et al.* 1980. Organochlorine pesticide, PCB, and PBB residues and necropsy data for bald eagles from 29 states—1975-77. Pestic. Monit. J. 13: 145-149.
Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. J. Mamm. 54: 14-32.
Mohr, C. E. 1972. The status of threatened species of cave-dwelling bats. Bull. Nat. Speleol. Soc. 34: 33-47.
Neter, J., and W. Wasserman. 1974. Applied Linear Statistical Models. Richard D. Irwin, Inc., Homewood, IL.
Reidinger, R. F., Jr. 1976. Organochlorine residues in adults of six southwestern bat species. J. Wildl. Manage. 40: 677-680.
Stebbins, R. E. 1970. Bats in danger. Oryx 10: 311-312.
Thomas, J. W. (Technical Ed.). 1979. Wildlife Habitats in Managed Forests—the Blue Mountains of Oregon and Washington. Agric. Handb. No. 553, USDA For. Serv.
Whitaker, J. O., Jr. 1972. Food habits of bats from Indiana. Can. J. Zool. 50: 877-883.
———, C. Maser, and L. E. Keller. 1977. Food habits of bats of western Oregon. Northw. Sci. 51: 46-55.

Received March 11, 1981
Accepted for publication April 10, 1981

Northwest Science

Volume 56, 1982

John W. Weber, Editor

Published by Northwest Scientific Association and Washington State University Press

Contents

Number 1 (February)

Small Mammals of a Bitterbrush-Cheatgrass Community 1
K. A. Gano and W. H. Rickard

The Trichoptera of Montana with Distributional and Ecological Notes 8
George Roemhild

Internal Parasites of Coyotes **(Canis latrans)** in Washington and Idaho 14
William J. Foreyt and Kristine M. Foreyt

Generic Relationships of **Phenacomys albipes** 17
Murray L. Johnson and Chris Maser

Population Structure of the Crab **Hemigrapsus oregonensis** 20
(Brachyura, Grapsidae) in Yaquina Bay Estuary, Oregon:
I. Reproductive Cycle
Robert E. Batie

Precipitation Variability in the Columbia Basin of Washington 27
J. D. Helvey and W. B. Fowler

Postburn Regrowth of Shrubs Related to Canopy Mortality 34
T. E. Owens

Self-Revegetation of Disturbed Ground in the Deserts of Nevada and Washington 41
W. H. Rickard and R. H. Sauer

Algal Growth Stimulus by Phosphorus in Flathead Lake, Montana, Sediments 48
William B. Perry and Jack A. Stanford

Photoperiod Experiments on the American Robin (**Turdus migratorius** L.) 53
D. Lynne Kemper and J. Mary Taylor

Contributions to Paleontology by an Early Montana Physician 58
Thomas H. Lewis

The Non-Fisheries Biological Resources of the Hanford Reach 62
of the Columbia River
W. H. Rickard, W. C. Hanson, and R. E. Fitzner

Association News 77

Number 2 (May)

Wintering Bald Eagles in Jackson Hole, Wyoming 79
Dennis R. Davenport and John L. Weaver

Nitrate and Ammonium Levels in Relation to Site Quality in Douglas-fir Soil and Litter 83
Daniel J. Vogt and Robert L. Edmonds

Bouguer Gravity Study of Enumclaw/Pinnacle Peak, Washington 90
Duncan S. Campbell and Daniel J. Johnson

Insects and Other Factors Affecting Noble Fir Seed Production at Two Sites in Oregon 101
J. H. Scurlock, R. G. Mitchell, and K. K. Ching

Numerical Phenetic Analysis of Variation in Populations of **Poa secunda** Presl. and **Bromus japonicus** Thunb. **(Poaceae)** 108
Bonnie Heidel, E. Jennifer Christy, and Amy Jean Gilmartin

The Relationship of Maximum Canopy Leaf Area to Forest Growth in Eastern Washington 121
Paul E. Schroeder, Brooks McCandish, Richard H. Waring, and David A. Perry

Opportunistic Feeding by Coyotes 131
Dirk Van Vuren and Stephen E. Thompson, Jr.

A Study of Surface Waters and Sediments in Southern Spokane County, Washington, for the Presence of **Yersinia enterocolitica** 136
Marion Bacon

Diets and Habitats of Mule Deer in South-central Washington 138
Daniel W. Uresk and Virginia A. Uresk

Inter- and Intrastream Migration of Cutthroat Trout **(Salmo clarki)** in Spawn Creek, a Tributary of the Logan River, Utah 148
David R. Bernard and Eugene K. Israelsen

Number 3 (August)

Wolverines in Western Wyoming 159
John H. Hoak, J. L. Weaver, and T. W. Clark

The Distribution of **Artemisia rigida** in Washington: A Challenge to Ecology and Geology 162
R. Daubenmire

Taste Aversion in Free Ranging Raccoons **(Procyon lotor)** 165
Lowell K. Nicolaus, Todd E. Hoffman, and Carl R. Gustavson

Effects of Volcanic Ash on Soil Nitrogen Mineralization and Accompanying CO_2 Production 170
J. L. Smith, E. J. Owens, and B. L. McNeal

Siphonaptera: Host Records from Crater Lake National Park, Oregon 176
Robert L. Gresbrink and David D. Hopkins

A Comparison of Treeless Areas in the Forested Foothills of the Cascade Mountains of Western Washington 180
Kern Ewing

The Distribution and Thickness of Volcanic Ash in Montana 190
Thomas J. Nimlos and Hans Zuuring

Dispersal, Daily Activity, and Home Range of Coyotes in Southeastern Idaho 199
Roger A. Woodruff and Barry L. Keller

Cervid Activity Patterns in Relation to Foraging Constraints: Western Washington 208
Thomas A. Hanley

Early Cenozoic Geology of Central Washington State: I. Summary of Sedimentary, Igneous, and Tectonic Events 218
Randall L. Gresens

Age Determination and Age-Specific Reproduction in Belding's Ground Squirrels 230
David B. Costain and B. J. Verts

Habitat Use by Porcupines in a Ponderosa Pine/Douglas-fir Forest in Northeastern Oregon 236
Graham W. Smith

Population Structure of the Crab **Hemigrapsus oregonensis** (Brachyura, Grapsidae) in Yaquina Bay Estuary, Oregon: II. Vertical Distribution, Biomass, and Production 241
Robert E. Batie

Primary Production and Canopy Cover in Bitterbrush-Cheatgrass Communities 250
W. H. Rickard and R. H. Sauer

Publication Announcement: 1981 Corvallis Forestry Symposium 257

Errata: Helvey, J. D., and W. B. Fowler 257
Northw. Sci. 56:27-33

Errata: Van Vuren, D., and S. E. Thompson, Jr. 257
Northw. Sci. 56:131-135

Number 4 (November)

Early Cenozoic Geology of Central Washington State: II. Implications for Plate Tectonics and Alternatives for the Origin of the Chiwaukum Graben 259
Randall L. Gresens

A Rapid Method for Analysis of Tissues for Heavy Metals Utilizing Atomic Absorption Spectrophotometry 265
Ronald J. Kendall and Patrick F. Scanlon

Taxonomic Extensions in the Chilcotin Mountains of Southern British Columbia 268
Corinne J. Selby and Michael D. Pitt

Soil Nitrogen Gradients as Influenced by Sagebrush Canopy in Southern British Columbia 276
S. J. Wikeem and Michael D. Pitt

A Prelininary Survey of Forest Bird Communities in Northern Idaho 287
Steven R. Peterson

Mule Deer and Elk Responses to Horsefly Attacks 299
William B. Collins and Philip J. Urness

Summer Raptor Populations of a Washington Coulee 303
Richard L. Knight and Dwight G. Smith

Winter Foods of Eastern Oregon Bobcats 310
Dale E. Toweill

Comparison of Phenological Patterns in Prairie and Subalpine Meadow Communities 316
Louise E. Jackson

Organochlorine Residues in Bats after a Forest Spraying with DDT 329
Charles J. Henny, Chris Maser, John O. Whitaker, Jr., and T. Earl Kaiser

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian D. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
F. A. Gilfillan
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Frank D. Nicol
Francis J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
S. C. Vandecaveye
Richard B. Walker
D. J. Wort

1982 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1982 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Gonzaga University, Spokane, Washington
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Malaspina College, Nanaimo, British Columbia, Canada
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Northern Montana College, Havre, Montana
Oregon College of Education, Monmouth, Oregon
Oregon Institute of Technology, Klamath Falls, Oregon
Oregon State University, Corvallis, Oregon
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
Saint Martin's College, Lacey, Washington
Seattle Central Community College, Seattle, Washington
Seattle Pacific University, Seattle, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
South Seattle Community College, Seattle, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Oregon, Eugene, Oregon
University of Puget Sound, Tacoma, Washington
University of Victoria, Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State University, Pullman, Washington
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Yakima Valley College, Yakima, Washington

1982 Sustaining Individual Members

Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Robert L. Carr, Cheney, Washington
Susan G. Conrad, Corvallis, Oregon
George W. Douglas, Victoria, British Columbia, Canada
Bruce Ettling, Vancouver, Washington
George R. Fahnestock, Seattle, Washington
Gerald H. Haddock, Wheaton, Illinois
Frederick C. Hall, Portland, Oregon
Charles R. Hatch, Moscow, Idaho
Robert J. Jonas, Pullman, Washington
Barry L. Keller, Pocatello, Idaho
Denis L. Lavender, Corvallis, Oregon
William L. Lester, Arcata, California
William A. Long, Crescent City, California
Albert L. Merkel, Moscow, Idaho
Daniel F. Milam, Bellevue, Washington
Emmett B. Moore, Jr., Richland, Washington
Milton M. Mosher, Pullman, Washington
William A. Rickard, Richland, Washington
Lee E. Rogers, Richland, Washington
Raymond A. Soltero, Cheney, Washington
Ronald J. Taylor, Bellingham, Washington
Daniel W. Uresk, Rapid City, South Dakota
Shepard M. Zedaker, Christiansburg, Virginia

Northwest Science

Washington State University

Pullman, Washington 99164

Associate Editors

Botany	Kenneth C. Swedberg	Eastern Washington University
Forestry	Arthur R. Tiedemann	U.S. Forest Service
Geology	Franklin F. Foit, Jr.	Washington State University
Soils	Stanley P. Gessel	University of Washington
Zoology	Irven O. Buss	Washington State University

Change of Address Send change of address notice to the Treasurer as listed on the inside front cover.

Instructions to Authors The pages of Northwest Science are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. At least one of the authors of papers submitted for publication must be a member of the Northwest Scientific Association. Manuscripts (original typescript plus two copies) should be submitted to the Editor, Northwest Science, Washington State University, Pullman, Washington. Prior to submitting manuscripts, authors should request a copy of "Instructions to Authors" from the Editor.

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164, U.S.A.